

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

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21 **Abstract**

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

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

52 The ventral pathway, commonly referred to as the ‘what’ pathway, is characterized by object  
53 feature selectivity and projects anteriorly from the occipital visual areas toward the hippocampus  
54 and the inferior temporal cortex (Kravitz et al., 2013). Damage to cortical regions along the  
55 ventral pathway results in visual agnosia, evidenced by difficulties in object recognition but  
56 preserved motor interactions with objects (Goodale & Milner, 1992; 1994; Karnath et al., 2009).  
57 Patients with ventral pathway damage but an intact dorsal pathway continue to manipulate,  
58 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

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

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

A	Fire Hydrant	Picture Frame	Window	Toilet	Candle	Garbage Can	Water Fountain	Potted Plant	Fan	Lamp
										
	0.010°	0.006°	0.008°	0.006°	0.010°	0.005°	0.018°	0.013°	0.006°	0.007°
	Snow Shovel	Handsaw	Plunger	Screw-driver	Hammer	Wrench	Knife	Bottle Opener	Spatula	Mug
										
	0.007°	0.011°	0.007°	0.012°	0.010°	0.007°	0.010°	0.008°	0.015°	0.010°

B	Fire Hydrant	Picture Frame	Window	Toilet	Candle	Garbage Can	Water Fountain	Potted Plant	Fan	Lamp
										
	0.010°	0.013°	0.012°	0.009°	0.009°	0.007°	0.011°	0.012°	0.007°	0.008°
	Snow Shovel	Handsaw	Plunger	Screw-driver	Hammer	Wrench	Knife	Bottle Opener	Spatula	Mug
										
	0.016°	0.018°	0.007°	0.014°	0.008°	0.009°	0.009°	0.009°	0.009°	0.013°

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

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

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

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



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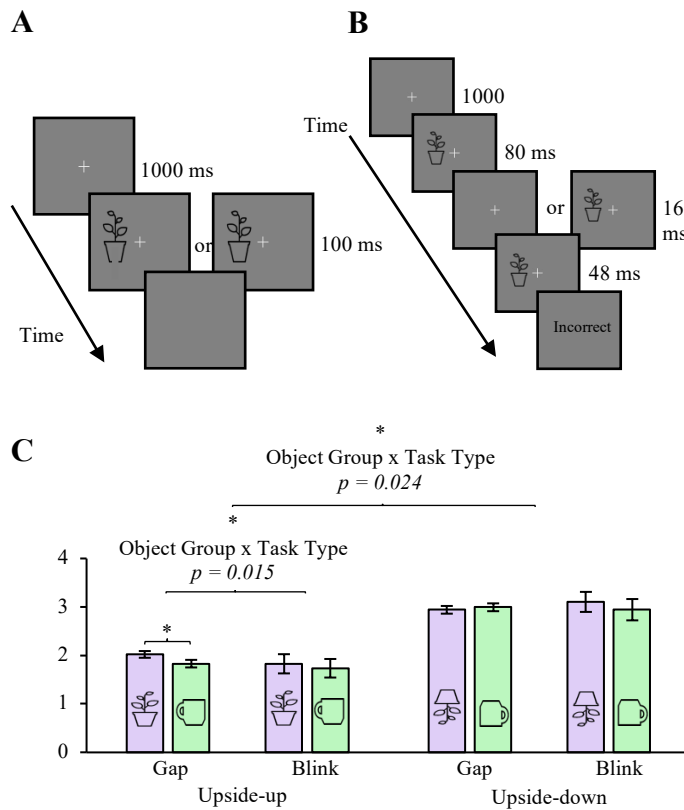


Figure 2. The paradigm and results for Experiments 1 and 2. Participants maintained fixation on the center cross. An object appeared to the left or right of fixation. A) For the spatial-gap paradigm, participants indicated by keypress if the bottom line of the presented object contained a gap. B) for 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 ( $M_{non-manipulable} = 2.021; M_{manipulable} = 1.831$ ). 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 ( $M_{non-manipulable} = 2.466; M_{manipulable} = 2.340$ ) (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.

159 The spatial and temporal paradigms used  $d'$  as a measure of perceptual sensitivity (Fig.  
 160 2). A two-way repeated-measures analysis of variance (ANOVA) was conducted on  $d'$  with  
 161 object group (manipulable, non-manipulable) and stimulus type (gap, blink) as within-subject  
 162 variables (Fig. 2C, left). The ANOVA revealed no significant main effect of object group ( $F(1,$   
 163  $25) = 2.342, p = 0.138, \eta_p^2 = 0.086$ ), and a significant main effect of task type ( $F(1, 25) =$   
 164  $50.953, p < 0.001, \eta_p^2 = 0.671$ ) such that  $d'$  sensitivity was higher for blinks than for gaps ( $M_{gaps}$   
 165  $= 1.93; M_{blinks} = 2.97$ ). Importantly, and consistent with the hypothesis of differential  
 166 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 ( $M_{\text{non-manipulable}} = 2.021; M_{\text{manipulable}} = 1.831$ ). 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).

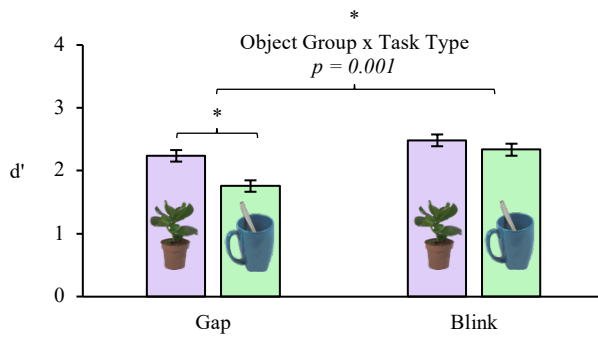
178 While Experiment 1 provides evidence for biased engagement of the ventral pathway for  
179 non-manipulable object perception during a temporal task, it could be argued that despite careful  
180 low-level feature controls (e.g., luminance, size, elongation) an uncontrolled low-level difference  
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-

190 level features of each object while impairing participants' ability to rapidly recognize and access  
191 their semantic knowledge of the objects' function. Inversion has been found to interfere with  
192 recognition of faces and objects (Diamond and Carey, 1986). Following from the hypothesis that  
193 semantic knowledge of object's utility drives the perceptual difference between manipulable and  
194 non-manipulable objects, we predict that object inversion should reduce the difference between  
195 manipulable and non-manipulable objects. A two-way repeated-measures ANOVA was  
196 conducted on  $d'$  with object group (manipulable, non-manipulable) and task type (gap, blink) as  
197 within-subject variables. The ANOVA revealed a significant main effect of object group ( $F(1,$   
198  $25) = 5.860, p = 0.023, \eta_p^2 = 0.190$ ) such that  $d'$  was higher for non-manipulable objects than for  
199 manipulable objects ( $M_{\text{non-manipulable}} = 2.466; M_{\text{manipulable}} = 2.340$ ) (Fig. 2C, right). There was also  
200 a significant main effect of task type ( $F(1, 25) = 82.298, p < 0.001, \eta_p^2 = 0.767$ ) such that  $d'$  was  
201 higher for blinks than for gaps ( $M_{\text{gaps}} = 1.782; M_{\text{blinks}} = 3.024$ ). As predicted, there was no  
202 significant interaction between object group and task type ( $F(1, 25) = 0.508, p = 0.483, \eta_p^2 =$   
203  $0.020$ ). In order to statistically demonstrate that results of the inversion experiment are indeed  
204 different from those observed in Experiment 1, data were subjected to a between-subject  
205 ANOVA with object orientation (upright, inverted) as a between subjects variable and object  
206 group and task type as within subject factors. The ANOVA revealed a significant three-way  
207 interaction between object group, task type, and orientation ( $F(1, 50) = 5.381, p = 0.024, \eta_p^2 =$   
208  $0.097$ ) such that, as predicted, orientation significantly reduced the effect for the inverted objects.

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

213 then non-manipulable objects will be biased to the ventral pathway leading to higher sensitivity  
214 (as measured by  $d'$ ) in the spatial gap task, replicating the pattern of performance observed in  
215 Experiment 1. A two-way repeated-measures ANOVA was conducted on  $d'$  with object group  
216 (manipulable, non-manipulable) and task type (gap, blink) as within-subject variables. The  
217 ANOVA revealed a significant main effect of object group ( $F(1, 29) = 28.211, p < 0.001, \eta_p^2 =$   
218  $0.493$ ) with non-manipulable objects having a higher sensitivity than manipulable objects ( $M_{\text{non-}}$   
219  $\text{manipulable} = 2.361, M_{\text{manipulable}} = 2.046$ ) (Fig. 3). There was also a significant main effect of task  
220 type ( $F(1, 29) = 8.413, p = 0.007, \eta_p^2 = 0.225$ ) with blinks having a higher average sensitivity  
221 than gaps ( $M_{\text{blinks}} = 2.409, M_{\text{gaps}} = 1.998$ ). Importantly, a two-way interaction between object  
222 group and task type was also significant ( $F(1, 29) = 13.061, p = 0.001, \eta_p^2 = 0.311$ ), driven by a  
223 simple main effect in the gap condition ( $F(1, 29) = 46.424, p < 0.001, \eta_p^2 = 0.616$ ) such that non-  
224 manipulable objects had a higher  $d'$  for gaps than did the manipulable objects ( $M_{\text{non-manipulable}} =$   
225  $2.238; M_{\text{manipulable}} = 1.758$ ). In order to statistically demonstrate that results observed using real  
226 objects are indistinguishable from the results observed using the line-drawings in Experiment 1,  
227 the data were subjected to a between-subject ANOVA with stimulus type (line drawings, real  
228 object images) as a between subjects variable and object group and task type as within subject  
229 factors. The ANOVA revealed no significant three-way interaction between object group, task  
230 type, and stimulus type ( $F(1, 54) = 0.454, p = 0.503, \eta_p^2 = 0.000159$ ). These results replicate  
231 Experiment 1, providing strong additional support for the hypothesis that the perceptual  
232 differences between manipulable objects and non-manipulable objects is due to the semantic  
233 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 ( $M_{\text{non-manipulable}} = 2.361, M_{\text{manipulable}} = 2.046$ ) (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 ( $M_{\text{blinks}} = 2.409, M_{\text{gaps}} = 1.998$ ). 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 ( $M_{\text{non-manipulable}} = 2.238; M_{\text{manipulable}} = 1.758$ ).

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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<sup>1</sup>. 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-

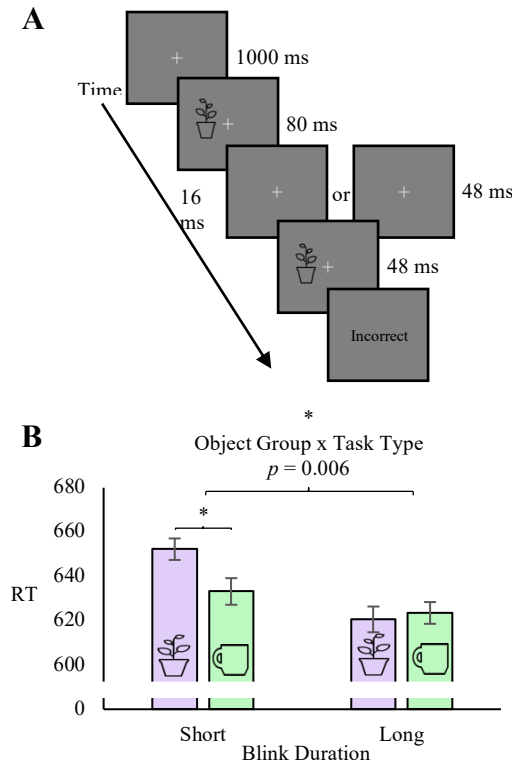
manipulable objects due to the increased magnocellular input, and therefore temporal resolution,

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

<sup>1</sup> We thank Ed Awh, from the University of Chicago, for the helpful suggestion.

248 conducted on RT with object group (manipulable, non-manipulable) and blink duration (short,  
 249 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;  $M_{long} = 621.997$  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 ( $M_{manipulables} = 633.150$ ;  $M_{non-manipulable} = 652.210$ ).

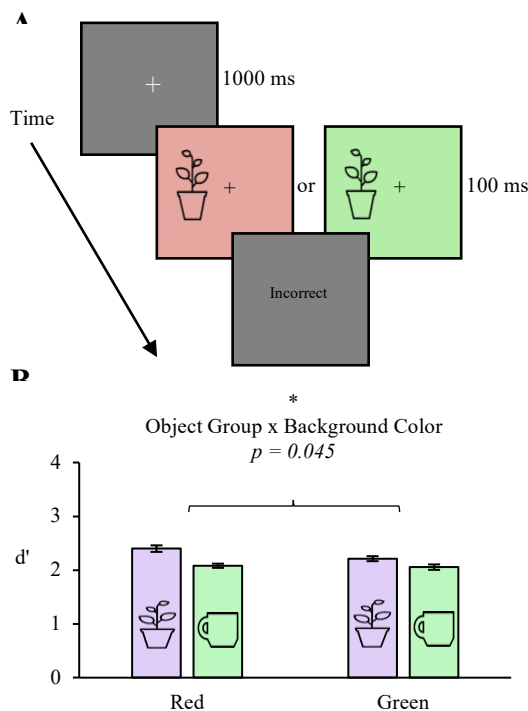
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251 The ANOVA revealed no significant main effect of object group ( $F(1, 24) = 4.080, p =$   
 252  $0.055, \eta_p^2 = 0.145$ ) (Fig. 4). There was a significant main effect of blink duration ( $F(1, 24) =$   
 253  $4.850, p = 0.038, \eta_p^2 = 0.168$ ) such that the short duration elicited a higher RTs than did the long  
 254 duration ( $M_{short} = 642.68$  ms;  $M_{long} = 621.997$  ms). The two-way interaction between object  
 255 group and blink duration was significant ( $F(1, 24) = 9.011, p = 0.006, \eta_p^2 = 0.273$ ) driven by a  
 256 simple main effect in the short blink condition ( $F(1, 24) = 11.710, p = 0.002, \eta_p^2 = 0.328$ ) such  
 257 that manipulable objects had a lower RT for short blinks than did the non-manipulable objects  
 258 ( $M_{manipulable} = 633.150$ ;  $M_{non-manipulable} = 652.210$ ). In accuracy, no effect was observed for object  
 259 group ( $F(1, 24) = 3.666, p = 0.068, \eta_p^2 = 0.133$ ), blink duration ( $F(1, 24) = 1.509, p = 0.231, \eta_p^2$

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

283 two-way repeated-measures ANOVA was conducted on  $d'$  with object group (manipulable, non-  
284 manipulable) and background color (green, red) as within-subject variables. The ANOVA  
285 revealed a significant main effect of object group ( $F(1, 25) = 17.171, p < 0.001, \eta_p^2 = 0.407$ )  
286 with non-manipulable objects having a higher average than manipulable objects ( $M_{\text{non-manipulable}} =$   
287  $2.25, M_{\text{manipulable}} = 2.02$ ) (Fig. 5B). There was no significant main effect of background color  
288 ( $F(1, 25) = 2.138, p = 0.156, \eta_p^2 = 0.079$ ) but, as predicted, there was a significant two-way  
289 interaction between object group and background color ( $F(1, 25) = 4.444, p = 0.045, \eta_p^2 = 0.151$ )  
290 such that the effect was increased with the red background. It was hypothesized that if the  
291 perceptual differences between manipulable and non-manipulable objects are mechanistically  
292 derived from the magno- and parvo-cellular processing in the two visual pathways, then  
293 suppression of the magnocellular processing with red light should modulate the effect. The  
294 results of Experiment 5 support our hypothesis by demonstrating an increase of the perceptual  
295 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 ( $M_{\text{non-manipulable}} = 2.25, M_{\text{manipulable}} = 2.02$ ). 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 ( $F(1, 25) = 4.444, p = 0.045, \eta_p^2 = 0.151$ ).



296

297           We hypothesized that manipulable and non-manipulable objects, due to differential  
298 recruitment of the two visual pathways, would elicit perceptual differences stemming from the  
299 characteristic spatial and temporal resolutions associated with the magno- and parvo-cellular  
300 inputs. In five experiments we provide strong evidence in support of behavioral consequences  
301 driven by physiological and anatomical differences of the two visual pathways, and argue that  
302 semantic knowledge of object utility guides processing along a particular pathway. If an object  
303 has a strong action association, its processing will be largely determined by activity in the dorsal  
304 pathway which is not found with objects that lack strong action association (Chao & Martin,  
305 2000; Noppeney et al., 2006; Mahon et al., 2007). The increased level of activity in the parietal  
306 regions endows the perception of action-associated objects with greater access to the information  
307 encoded in the magnocellular channel which preferentially courses through the dorsal pathway.  
308 Without the enhanced dorsal pathway activity evoked by action associations, object  
309 representation is more dependent on the ventral pathway, which has a higher ratio of  
310 parvocellular channel information than does the dorsal pathway (Maunsell et al., 1990; Baizer et  
311 al., 1991; Ferrera et al., 1992). Based on differential magno- and parvo-cellular input to the two  
312 pathways, we predicted that the perception of objects with strong action associations results in an  
313 increased temporal resolution and that the perception of objects without such associations results  
314 in an increased spatial resolution. In the experiments reported here, we offer evidence that  
315 objects are perceived with different spatial and temporal resolutions depending on object  
316 semantic knowledge (namely, whether the object is manipulable or non-manipulable). In two  
317 follow-up control experiments, further evidence was provided in support of the hypothesis that  
318 the difference between manipulable and non-manipulable objects in the spatial task was driven

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

328         Results are strengthened by a set of various low-level controls imposed on the stimulus  
329 set. Manipulable and non-manipulable object groups were controlled for size, hue, saturation,  
330 visual clutter, and image value. Additionally, object groups were controlled for the degree of  
331 elongation difference (i.e., aspect ratio) as this factor has been shown to drive some amount of  
332 dorsal visual pathway selective for tools, which are a subset of manipulable object (Chen et al.,  
333 2018).

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

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

356           A possible mechanism linking the near-hand effect reported by Gozli et al. (2012) and the  
357 perceptual difference between manipulable and non-manipulable objects derive from the bimodal  
358 cells in the anterior parietal cortex (Graziano & Gross, 1993). The bimodal cells have a  
359 somatosensory receptive field covering a part of the hand and they have a visual receptive field  
360 corresponding to a part of the visual field near their associated hand area. When an object is  
361 shown, if that object does not have a strong action association, then the activity of the bimodal  
362 cells is unaffected. After the organism has learned to use the object with their hands, the bimodal  
363 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

385 **Methods**

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

391 For experiment 1, 26 undergraduate students (19 female; average age: 19.2; 6 left-  
392 handed) were recruited. No participant was removed from the analyses. For experiment 2, 27  
393 undergraduate students were recruited. Twenty-six participants' data (14 female; average age:  
394 19.0; 1 left-handed) were analyzed after one participant was cut for below chance accuracy in  
395 one of the conditions. For experiment 3, 33 undergraduate students were recruited. Thirty  
396 participants' data (26 female; average age: 19.07, 3 left-handed) were analyzed after eight  
397 participants were cut for below chance accuracy in at least one of the conditions. For experiment  
398 4, 34 undergraduate students were recruited. Twenty-five participants' data (14 female; average  
399 age: 19.0; 1 left-handed) were analyzed after six participants were cut for not finishing the  
400 experiment and nine participants were cut for having less than chance accuracy in at least one of  
401 the conditions. For experiment 5, 26 undergraduate students were recruited. Twenty-five  
402 participants' data (18 female; average age: 19.5, 0 left-handed) were analyzed after one  
403 participant was cut for chance accuracy in all conditions.

404

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

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

417           Objects were controlled for low-level differences by calculating the mean luminance, size,  
418 and aspect ratio (i.e., measure of elongation) for each object. There was no mean luminance  
419 difference between object groups, an independent samples t-test ( $t(18) = -0.960, p = 0.350$ ). There  
420 was no significant difference in mean size (t-test ( $t(18) = 1.043, p = 0.311$ ), or aspect ratio ( $t(18)$   
421  $= 1.209, p = 0.242$ ). The width of the bottom line was controlled for each object on which the gap  
422 appeared. There was no significant difference between manipulable and non-manipulable objects  
423 in bottom line width in an independent samples t-test ( $t(18) = 0.922, p = 0.369$ ).

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

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

440

441 **Design and Procedure.** In Experiment 1, each trial began with a single central fixation point,  
442 which subtended a visual angle of  $1^\circ \times 1^\circ$ . The central fixation point was rendered in white (HSV  
443  $= 0, 0, 100$ ). After 1000 ms of fixation presentation, a single object line drawing would appear  $4^\circ$   
444 to the left or right of the fixation point. The side of presentation was counterbalanced such that  
445 each participant saw an equal number of stimuli on the left and on the right. The stimuli were  
446 displayed as large as possible within a  $4^\circ \times 4^\circ$  area and all stimuli were presented in color on a  
447 dark gray background (HSV  $= 0, 0, 50$ ). All objects are displayed in Figure 1.

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

453           A staircase procedure was used to calibrate the size of the gap to each object to ensure that  
454 the gap was equally perceptible across each object regardless of each objects' individual  
455 characteristics (Pelli and Bex, 2013). Sixteen undergraduate students (13 female; average age: 18.8;  
456 4 left-handed) from the George Washington University participated in exchange for course credit.  
457 In each trial the object would be presented with or without the spatial gap which would begin with  
458 a size of 0.025° visual angle. If the gap was detected correctly for two consecutive trials, the gap  
459 decreased by one 0.005° step. If the gap was missed, or a false alarm was made to the absence of  
460 a gap, for two consecutive trials, the gap was increased by one 0.005° step. The gap was calibrated  
461 until twenty trials had been completed or until the staircase reversed direction (2 correct followed  
462 by 2 incorrect or vice versa) three times. The gap size for each object is displayed in figure 1.

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

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

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



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

488 Experiment 4 was similar in trial structure to the temporal blink condition of Experiment  
489 1, except instead of temporal blink detection each trial had a temporal blink that was either short  
490 or long in duration. The objects had an equal probability of having a short or a long temporal  
491 blink. In the short blink condition, the object first appeared for 96 ms, followed by a 16 ms  
492 temporal blink, and then the object appeared a second time for 32 ms. In the long blink  
493 condition, the object first appeared for 64 ms, followed by a 48 ms temporal blink, and then the  
494 object was presented for a second time for 32 ms. Participants were to report a presence of a  
495 short temporal blink by pressing the 'c' key and a long temporal blink by pressing the 'm' key on  
496 the keyboard. Feedback was presented exclusively on incorrect trials. Participants completed a  
497 total of 720 trials broken into 6 blocks, 360 trials of short blink duration and 360 trials of long  
498 blink duration.

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

505

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

513

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

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

518

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