## Report

# Representation of Object Weight in Human Ventral Visual Cortex

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#### Summary

Skilled manipulation requires the ability to predict the weights of viewed objects based on learned associations linking object weight to object visual appearance [1-5]. However, the neural mechanisms involved in extracting weight information from viewed object properties are unknown. Given that ventral visual pathway areas represent a wide variety of object features [6-11], one intriguing but as yet untested possibility is that these areas also represent object weight, a nonvisual motor-relevant object property. Here, using event-related fMRI and pattern classification techniques, we tested the novel hypothesis that object-sensitive regions in occipitotemporal cortex (OTC), in addition to traditional motor-related brain areas, represent object weight when preparing to lift that object. In two studies, the same participants prepared and then executed lifting actions with objects of varying weight. In the first study, we show that when lifting visually identical objects, where predicted weight is based solely on sensorimotor memory, weight is represented in object-sensitive OTC. In the second study, we show that when object weight is associated with a particular surface texture, that texture-sensitive OTC areas also come to represent object weight. Notably, these texture-sensitive areas failed to carry information about weight in the first study, when object surface properties did not specify weight. Our results indicate that the integration of visual and motor-relevant object information occurs at the level of single OTC areas and provide evidence that the ventral visual pathway is actively and flexibly engaged in processing object weight, an object property critical for action planning and control.

#### Results

A single group of participants (n = 13) performed two real-action event-related fMRI studies in which, on each trial, they grasped and lifted a centrally located object that could be one of two weights: heavy (7.7 N) or light (1.9 N). Participants were first visually presented with the object, and then, following a delay period, they executed the action. The delayed timing of this task enabled us to isolate the

premovement responses (plan epoch) from the movement execution responses (execute epoch; see Figure 1 and Figure S1 available online) and then examine, using fMRI decoding methods, whether we could predict, on a given trial, the upcoming weight of the object to be lifted from the premovement voxel activity patterns.

#### Study 1

In study 1, the heavy and light objects were visually identical, and thus knowledge of object weight could only be acquired through previous lifts of that object (termed sensorimotor memory [12]). To acquire this knowledge, in each experimental run, participants first learned the weight of an object by lifting and replacing it six times directly in succession (interaction phase) before performing a series of six individual plan-and-lift trials with that same object (see Figure S1B for protocol). Behavioral control experiments showed that participants reliably learned object weight during the interaction phase and then used this knowledge to predict object weight on each single event-related trial (see Figure S2).

As a first test of whether it is even possible to decode, using brain activity, object weight information prior to movement, we analyzed the plan epoch activity patterns in three key somatomotor regions of interest (ROIs) in which object weight information is expected to be represented: contralateral primary motor cortex (M1), dorsal premotor cortex (PMd), and somatosensory cortex (SSc) [5, 13-16]. A voxel-wise contrast of execute > planning [collapsed across object weight; execute (heavy object + light object) > planning(heavy object + light object)] was used to localize these ROIs in individual participants, and the spatial activity patterns during the plan and execute epochs from these ROIs provided inputs to the pattern classifiers (see gray-shaded bars in Figure 2A for the time windows used for decoding; see Figure S3A for brain areas). Despite highly overlapping signal amplitude responses during planning, we found that the spatial activity patterns in these regions reliably discriminated the weight of the object to be lifted. In M1 and PMd, we found reliable decoding during the plan epoch (M1:  $t_{12} = 4.711$ , p = 0.001; PMd:  $t_{12} = 2.633$ , p = 0.022), whereas in SSc, consistent with the hand's mechanoreceptors being stimulated only at movement onset/object contact, reliable decoding only emerged during the execute epoch  $(t_{12} = 4.338, p = 0.001; see Figure 2A)$ . The expected results demonstrate the validity of our experimental approach and provide assurances of data quality.

Encouraged by these results, we next tested our main hypotheses by extracting the plan epoch activity from the object-sensitive lateral occipital complex (LOC) in the ventral visual pathway, a general functional region that can be putatively subdivided into the lateral occipital (LO) area and posterior fusiform sulcus (pFs) [6, 17, 18]. Areas LO and pFs were localized in each participant in a separate fMRI testing session based on their responses to intact versus scrambled objects (see the Supplemental Experimental Procedures). Despite the fact that visual cues about the object alone could not be used as a reliable indicator of its weight (because the objects were visually identical), we found that premovement activity patterns from both regions reliably predicted the weight of the object to be lifted (left LO,  $t_{12} = 3.086$ , p = 0.009; right LO,  $t_{12} = 3.355$ ,

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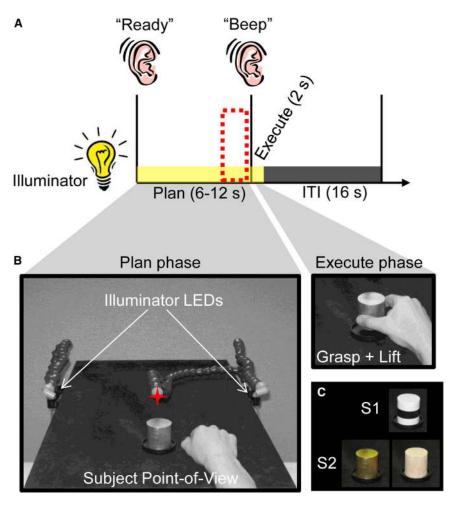


Figure 1. Methods

(A) Timing of each event-related trial. Trials began with the 3D object being illuminated concurrently with the auditory instruction "ready" being played through headphones. These events initiated the plan epoch of the trial. Following a jittered delay interval (6–12 s), subjects were then cued (via an auditory "beep") to perform the grasp-and-lift action (initiating the execute epoch). At 2 s after this cue, vision of the workspace was extinguished, and participants waited for the following trial to begin (16 s; intertrial interval [ITI]).

(B) Experimental setup, shown from the subject's point of view, time locked to events in (A). Plan epoch is shown in the left view, and execute epoch is shown in the right. Note that the centrally located target object never changed position from trial to trial. The red star represents the fixation light-emitting diode (which was foveated during data collection). Multivoxel pattern analysis (MVPA) was performed on single trials (using a leave-one-run-out cross-validation) and based on the windowed average of the percent signal change response corresponding to the plan and execute epochs (see Figure 2). To examine whether object weight information was represented in voxel activity patterns prior to movement onset, fMRI decoding from the premovement time points (bordered in dashed red line in A) was of critical interest.

(C) Objects used in study 1 (S1) and study 2 (S2). Each object could be one of two weights: heavy (7.7 N) or light (1.9 N).

See also Figure S1.

p = 0.006; left pFs,  $t_{12}$  = 2.270, p = 0.042; right pFs,  $t_{12}$  = 2.788, p = 0.016; Figure 2B).

To rule out the possibility that decoding of object weight information in areas LO and pFs arises from general visual attention differences associated with preparing to lift heavy versus light objects or from subtle differences in the visual appearance of the two objects, we next examined whether we could decode weight information from early visual areas V1 (primary visual area) and V2 (secondary visual area)—the activity of which is highly sensitive to spatial attention and visual differences between stimuli [6, 19, 20]. To localize the retinotopic location in V1/V2 that directly corresponds to the position of the target object, at the end of the study 1 testing session, we placed hollow semiopaque illuminable objects at (1) a location at which the target object appeared (lower visual field, bottom position) and (2) a location outside of reach that was never acted upon throughout the experiment (upper visual field, top position; see the Supplemental Experimental Procedures for further details). According to a block-design protocol, these two illuminable objects alternated flickering in an on-off fashion (at 5 Hz), resulting in a highly robust and reliable localization of the two object positions in V1/V2 within each subject (see Figure S4; note that the boundaries of V1 and V2 were defined in a separate localizer testing session using standard retinotopic mapping procedures; see the Supplemental Experimental Procedures). Importantly, when we extracted from these independently defined areas the plan epoch signals

corresponding to the lifting task, we found no decoding for object weight (Figure S4). Thus, it appears that the

representation of object weight emerges only in higher-order brain regions located further along the continuum of visual processing in occipitotemporal cortex (OTC) [6]. Additional behavioral control experiments indicated that participants maintained stable fixation throughout the task and could not visually discriminate the heavy and light objects, as evidenced by both their lifting behavior and perceptual reports (see Figures S1D and S1E). Taken together, these control fMRI and behavioral findings suggest that simple attention-related effects or object visual cues cannot account for the weight-sensitive activity observed in LOC.

#### Study 2

When lifting objects, people can exploit well-learned memory associations between object texture and weight to scale their lifting forces. For instance, people apply greater load force when lifting an object that appears to be made of brass than when lifting a similarly sized object that appears to be made of wood [3, 4, 21]. In addition, people can also learn new associations between texture and weight and use this knowledge to scale lifting forces accordingly [3, 4]. However, it is not known—once the association has been learned—how an object's texture and its weight become bound together at the level of neural mechanisms. Study 2 tested the hypothesis that OTC areas involved in texture processing [9], located posteriorly in lateral occipital cortex and anteriorly in a region of the collateral sulcus (CoS), also come to represent object

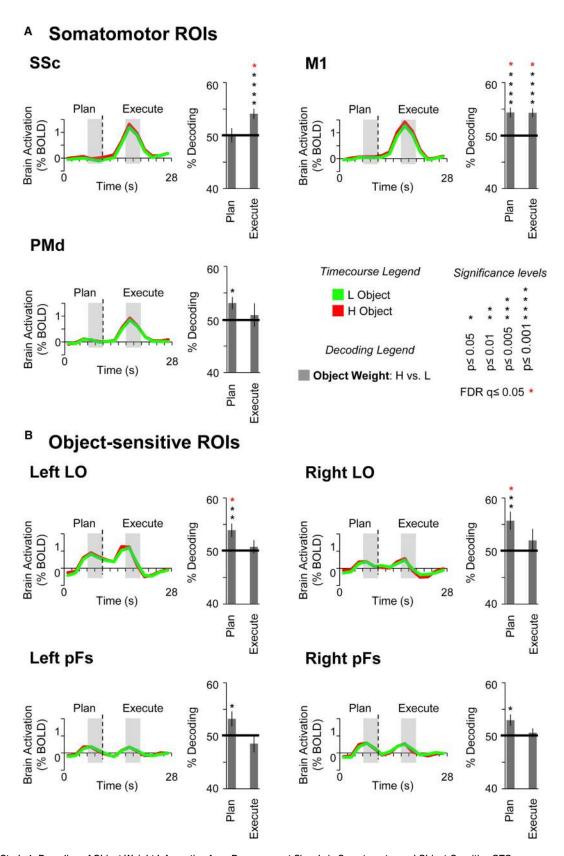


Figure 2. Study 1: Decoding of Object Weight Information from Premovement Signals in Somatomotor and Object-Sensitive OTC

Somatomotor cortex (A) and object-sensitive OTC (B). Each ROI is associated with two plots of data. The left data plots show percent signal change time course activity. The activity in each plot is averaged across all voxels within each ROI and across participants. Note that due to jittering of the delay period in the event-related design, to allow alignment, only time courses for five imaging-volume (10 s) delay periods are shown. Vertical dashed line corresponds to the onset of the execute epoch of the trial. Shaded gray bars indicate the two imaging-volume (4 s) windows that were averaged and extracted for MVPA. In the

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weight when weight information can be reliably derived from (and thus linked to) object texture.

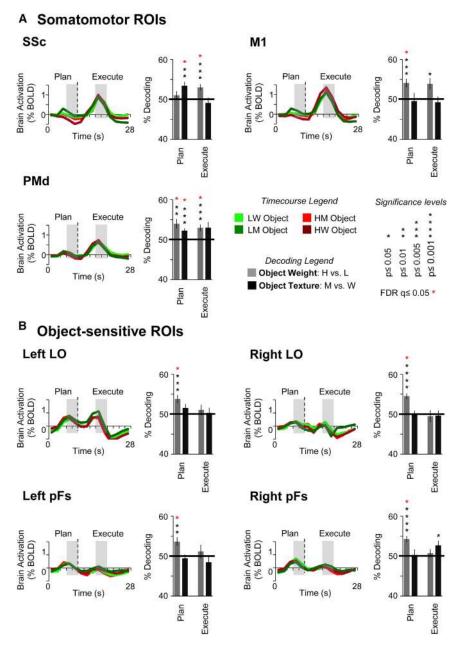
To test this prediction, study 2 was divided into interrelated experiments. In the first experiment, participants prepared, grasped, and then lifted two objects with a normal weighttexture mapping: a heavy metal and a light wood object (Figure 1C; objects were of the same weight as in study 1). Because weight and texture are directly linked in this first experiment, if we were able to decode differences between the two objects, it would be unclear whether knowledge of object weight or texture was responsible for driving such effects. Thus, to decouple these two object properties, in a second experiment, participants prepared, grasped, and then lifted two objects with the inverted weight-texture mapping: a heavy wood and a light metal object. By combining the data across the two experiments, we could partially disentangle activity patterns linked to a representation of object weight (i.e., test for a main effect of heavy versus light, independent of the object texture that cued weight on a particular trial) from those linked to a representation of object texture (i.e., test for a main effect of metal versus wood, independent of the weight cued by the object's texture on a particular trial). Both of these experiments were performed in the same testing session, and participants performed the normal weight-texture mapping experiment first so that we could examine effects that generalized across mappings (i.e., from the familiar to the arbitrary mappings). Importantly, prior to beginning the second experiment of study 2, participants lifted each object 15 times in the scanner ("learning phase") in an alternating fashion such that they fully learned the new texture-weight associations and scaled their lift forces accordingly (see Figure S1C). Thus, in both experiments in study 2, participants could reliably predict object weight based on texture visual cues (note that this was not the case in study 1).

We fixed the order in which participants experienced the two experiments in study 2 for two important reasons. First, although we are interested in distinguishing between welland newly learned texture-weight associations in future work (which would require extensive training such that newly learned associations become well learned), at this point, our aim was to test the neural representation of weight-texture associations independent of the precise nature of these associations. Second, had we counterbalanced the order of experiments across participants, we would introduce a serious potential confound. Specifically, we were concerned that if participants experienced the inverted (and arbitrary) texture-weight objects first, then they may have subsequently treated the normal textureweight objects as similarly arbitrary texture-weight objects (unlike the group of participants who experienced the normal objects first). By using a fixed order, we ensured that all participants experienced both normal and arbitrary texture-weight mappings. Of course, a limitation of this fixed-order design is that we cannot identify texture-sensitive areas that only represent well-learned or newly learned associations between texture and weight (though, as noted above, this same limitation might also extend to a design in which the order of experiments was counterbalanced). Critically, however, this design does enable us to identify texture-sensitive areas that represent weight independent of whether the association between texture and weight is well or newly learned.

To disentangle activity patterns related to object weight and texture in study 2, we performed two separate and independent decoding analyses. In the first analysis, all trials were analyzed only according to object weight. That is, regardless of the object texture linked to weight on a particular trial, the trials were classified solely on the basis of whether the object presented was heavy or light. In the second analysis, all trials were analyzed only according to object texture. That is, regardless of the object weight linked to texture on a particular trial, the trials were classified solely on the basis of whether the object presented was metal or wood. Accordingly, statistically significant classification in the first analysis will be based only on differences in the neural representation of weight information (and independent of the texture that cued weight), and in the second analysis, it will be based only on differences in the neural representation of texture information (and independent of the weight linked with the texture). We expected that a brain area involved in integrating signals related to object texture and weight during planning might show sensitivity to each of these separate object properties during the plan epoch.

We first considered the premovement activity patterns in the same somatomotor areas localized and examined in study 1. In PMd, we found main effects of both weight and texture during the plan epoch (weight:  $t_{12} = 3.349$ , p = 0.006; texture:  $t_{12} =$ 3.640, p = 0.003; see Figure 3A). This finding suggests that PMd is involved in integrating information about texture and weight, and expands upon previous evidence demonstrating its involvement in several aspects of visual-motor integration [15, 22-24]. As expected, we further found that, during both planning and execution, M1 represented object weight but not object texture (plan, weight:  $t_{12} = 3.884$ , p = 0.002; execute, weight:  $t_{12} = 2.831$ , p = 0.015; see Figure 3A). Notably, we further found that during planning, SSc represented object texture (texture:  $t_{12} = 3.312$ , p = 0.006; see Figure 3A), but not weight (the latter fully consistent with the results of study 1). Emerging evidence suggests that the primary sensory cortices (e.g., SSc) may represent information relevant for their modality (e.g., touch) despite that information arising through different sensory systems (e.g., vision) [25-28]. One intriguing though speculative interpretation suggested by our findings here is that SSc perhaps anticipates, based on visual cues about object texture (metal versus wood), differences in the tactile input to be experienced once the fingertips contact the object.

We next investigated our main hypotheses by extracting the study 2 plan epoch activity from LOC and from texture-sensitive brain regions in OTC. The latter areas, situated lateral to the CoS (lateral region) and anteriorly along the CoS (ventral region), were independently identified in each participant using a recently developed localizer task [7], performed in a separate testing session, based on the contrast of object textures and ensembles versus their scrambled counterparts. As predicted, we found that, as in study 1, weight information could be decoded from both areas LO and pFs during planning, showing that LOC also represents weight when it can be derived from texture (left LO, weight:  $t_{12} = 3.657$ , p = 0.003; right LO,



weight:  $t_{12}$  = 6.294, p < 0.001; left pFs, weight:  $t_{12}$  = 3.337, p = 0.006; right pFs, weight:  $t_{12}$  = 5.600, p < 0.001; see Figure 3B). However, we found that information about object texture could not be reliably decoded from LOC, consistent with accounts suggesting that the area is not involved in representing object texture [9]. By contrast, when we examined planning-related activity from the texture-sensitive brain regions, we found that these areas carried information about both weight and texture (left-lateral region, weight:  $t_{12}$  = 4.991, p < 0.001; texture:  $t_{12}$  = 4.016, p = 0.002; right- lateral region, weight:  $t_{12}$  = 5.558, p < 0.001; texture:  $t_{12}$  = 3.051, p = 0.010; left-ventral region, weight:  $t_{12}$  = 3.653, p = 0.003; right-ventral region, weight:  $t_{12}$  = 5.611, p < 0.001;

One intriguing possibility stemming from this result is that the texture-sensitive regions may only represent object weight when weight information can be reliably derived from

texture:  $t_{12} = 4.575$ , p = 0.001; see Figure 4).

Figure 3. Study 2: Decoding of Object Weight and Texture Information from Premovement Signals in Somatomotor and Object-Sensitive OTC Somatomotor cortex (A) and object-sensitive OTC (B). Percent signal change time courses and decoding accuracies are plotted and computed the same as in Figure 2. L, light; H, heavy; W, wood; M, metal. See also Figure S3.

the object's visual surface features (e.g., texture). To provide a key test of this idea, we examined whether object weight could be decoded from the texture-sensitive regions using the data from study 1. Recall that in study 1, the heavy and light objects were visually identical, and thus, weight could not be derived from object visual surface cues. Critically, when we extracted the study 1 data from the texture-sensitive regions, we found no evidence of weight decoding (see Figure 4). This suggests that object texture-sensitive areas may only be recruited to represent weight information when it is predictably linked to object visual appearance through learned sensorimotor associations.

To provide a further control, we next tested for the representation of object weight information in early visual areas V1/V2, localized using the same retinotopic mapping methods employed in study 1. Consistent with the results of study 1, we found that weight information could not be decoded from the early visual areas (see Figure S4). This finding reaffirms the notion that weight information emerges only in higher-order areas of the ventral visual pathway. Notably, however, we did find that object texture information could be reliably decoded from the V1/V2 ROI defined by the target object's actual location throughout the study 2 experiments (bottom object

position; texture:  $t_{12} = 10.142$ , p < 0.001; see Figure S4). This result is fully consistent with retinotopic early visual cortex showing sensitivity to the visual features of objects (in this case, texture [6]).

#### Discussion

Here, we show that object-sensitive OTC regions, in addition to traditional motor-related brain areas, represent object weight information when preparing to lift an object. This finding contributes to advancing our understanding of visual object processing in two key ways. First, our results demonstrate that the mechanical properties of an object, which are not directly available through vision, are represented in the ventral visual pathway, which is thought to be primarily involved in processing visual object properties. Second, our results indicate that ventral pathway areas, traditionally

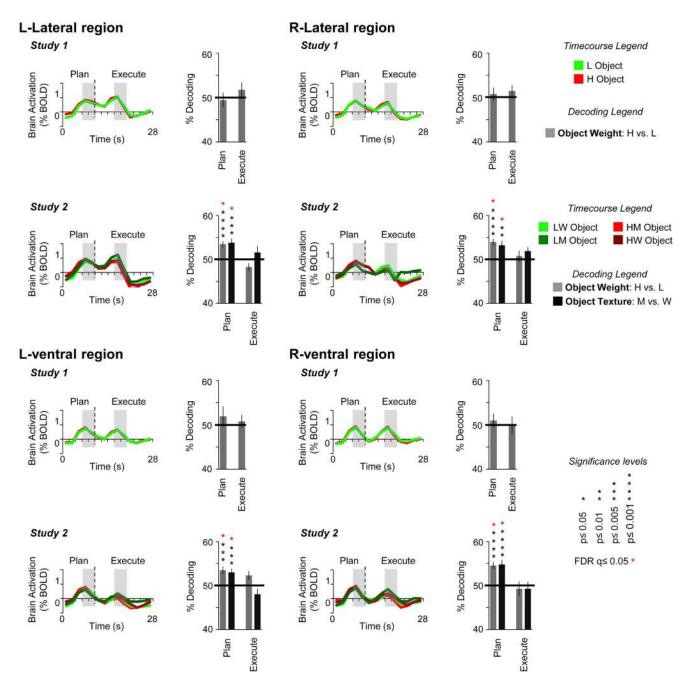


Figure 4. Studies 1 and 2: Decoding of Object Weight and Texture Information from Premovement Signals in Texture-Sensitive OTC

Percent signal change time courses and decoding accuracies are plotted and computed the same as in Figure 2. L, light; H, heavy; W, wood; M, metal. See also Figure S4 and Table S2.

associated with their role in visual perception and object recognition, are involved in processing object features critical for motor control, processing that traditionally has been thought to be the purview of the dorsal pathway.

The idea that distinct neural pathways support object processing for the purposes of action and perception [29, 30] arose primarily from studies examining reaching and grasping movements directed toward objects, where the relevant object properties (e.g., location and shape) can be directly appreciated through vision. Skilled object manipulation, however, requires knowledge of an object's properties relevant to

dynamics (e.g., weight), which cannot be reliably derived from vision alone and must instead be estimated based on stored knowledge linking visual information about the object (e.g., texture and identity) to weight [1–5]. It is clear that OTC structures represent visual object properties, such as size and texture [6, 8, 9], that are often correlated to weight [3]. Moreover, recent work has shown that OTC also represents the real-world (i.e., nonretinal) size of objects [31], information that would be important for computing object weight. Finally, there is accumulating behavioral evidence that visual information from the ventral visual pathway can influence estimations

of weight for lifting [32, 33]. Thus, one possibility, consistent with the proposed division of neural processing for the purposes of action and perception [29, 30], is that the ventral stream merely supplies the dorsal stream with visual object information (e.g., size, texture) used for computing weight. If this were the case, then the representation of weight information should only emerge at the level of frontoparietal cortex. Instead, here, we show that object weight, once learned, is actually represented at the level of object-processing regions in the ventral visual pathway. Moreover, we show that brain areas involved in processing the surface properties of an object (i.e., texture) come to represent the mechanical properties of that object (i.e., weight), but only when those two features become reliably linked through learning. Thus, the ventral visual pathway itself appears to be directly involved in processing both the surface and mechanical properties of an object and flexibly representing learned associations between those different object features.

A number of studies have provided evidence for sensitivity to both surface and material properties in medial regions of the ventral visual pathway. Cavina-Pratesi and colleagues [34, 35] reported a texture-specific region along a posterior aspect of the CoS, and Cant and colleagues have demonstrated sensitivity to both surface (i.e., color and texture [7, 8, 36]) and material properties (i.e., compliance [7]) in more anterior aspects of the CoS (which notably overlaps with some of object-sensitive pFs). Recently, responses in medial regions of both the human and monkey visual systems have been implicated in high-level perception of the visuotactile properties of materials (e.g., roughness, compliance), in contrast to the responses found in early visual areas, which are correlated more with low-level image properties of materials (e.g., spatial frequency [10, 11]). The representation of weight information in the anterior surface-sensitive areas of Cant and colleagues [7], as reported here, is in line with the suggestion that these regions are involved in the integration of multiple object features so as to form more high-level conceptual representations of objects. In this view, posterior regions selective for one particular surface property (e.g., texture), like that of Cavina-Pratesi and colleagues [34, 35], may be involved more in visual representations of objects, whereas these more anterior, higher-level representations may instead be flexibility used to support computations of both the motor and visual systems. However, because these medial regions encompass a large extent of the CoS and the current study did not directly localize the texture-specific posterior CoS (as in [34, 35]), it is unclear the extent to which these regions described above may perform distinct roles, and future studies will be needed to provide direct comparisons.

Are there other factors that may account for the present results? One possibility is that the activity patterns in OTC, rather than representing weight information, may be due to general differences in visual attention between the heavy and light objects. We tested for this possibility by examining activity in the retinotopic location of early visual cortex corresponding to the position of the target objects in studies 1 and 2. Given that early visual cortex is highly sensitive to differences in the allocation of attention (e.g., [20]), we would have expected—if attention had a strong modulating effect on the findings in OTC—to observe similar findings in early visual areas as in OTC. Although we did not find decoding of heavy versus light objects from early visual cortex signals, the abstract nature of representations in higher-level visual cortex makes it difficult to completely rule out any attention-related effects. Another

possible explanation of the results is that OTC may instead be representing material density (this may especially be the case in the texture-sensitive regions). Given that all the objects used in the current studies were of the same size, we are unable to distinguish between neural representations of weight versus density. Another potential limitation of the current studies is that only two object weights were used. Although this manipulation was done for practical reasons (i.e., to limit the number of possible trial types and, thus, increase their statistical power), it is unclear the extent to which the decoding observed in OTC reflects a categorical representation of weight information (e.g., an object is either heavy or light) versus a continuous representation of weight (e.g., changes in activity patterns that directly correspond to changes in object weight). Future studies testing for systematic shifts in activity patterns across a wider range of object weights will be required to disentangle these possibilities. Lastly, we also cannot exclude that what is being represented in several brain areas during planning are features often correlated to weight, rather than weight itself. Weight information in the context of sensorimotor control is used to modulate the fingertip forces applied to objects and to anticipate the tactile responses to be experienced by the fingertips at object liftoff (for review, see [5]). Certainly, claims about the representation of such sensorimotor information in brain areas like M1 and S1, respectively, are unlikely to be controversial. What remains unclear, however, is the extent to which this same kind of sensorimotor information is represented in OTC. Future studies, involving lesions or transcranial magnetic stimulation methods, will be required to probe the causal role of the weight information represented in ventral visual structures.

Why should an object feature like weight be represented in the ventral visual pathway? Whereas the dorsal visual pathway is thought to be involved in computing real-time motor commands based on directly viewed object metrics, as when reaching toward objects, the ventral pathway is thought to extract lasting and detailed information about objects via memory associations and recognition [29, 30]. Moreover, visual areas appear to also represent arbitrary associations between paired viewed objects [37] and between viewed objects and arbitrary actions performed with those objects [38]. Thus, the ventral visual stream appears to be well suited for representing learned, and often quite labile, associations between object visual features and weight, which can then be used to extract weight information for the purposes of object lifting and manipulation. Expanding upon the simpler notion that OTC areas may only be involved in general purpose object-related processing for a role in pure perception, our findings suggest that these areas may perform an even more universal role: integrating object knowledge acquired through vision and sensorimotor experience for the purpose of guiding action and behavior.

### **Supplemental Information**

Supplemental Information includes Supplemental Experimental Procedures, four figures, and two tables and can be found with this article online at http://dx.doi.org/10.1016/i.cub.2014.06.046.

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