Understanding the Dorsal and Ventral Systems of the Human Cerebral Cortex

Beyond Dichotomies

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Traditionally, characterizations of the macrolevel functional organization of the human cerebral cortex have focused on the left and right cerebral hemispheres. However, the idea of left brain versus right brain functions has been shown to be an oversimplification. We argue here that a top–bottom divide, rather than a left–right divide, is a more fruitful way to organize human cortical brain functions. However, current characterizations of the functions of the dorsal (top) and ventral (bottom) systems have rested on dichotomies, namely where versus what and how versus what. We propose that characterizing information-processing systems leads to a better macrolevel organization of cortical function; specifically, we hypothesize that the dorsal system is driven by expectations and processes sequences, relations, and movement, whereas the ventral system categorizes stimuli in parallel, focuses on individual events, and processes object properties (such as shape in vision and pitch in audition). To test this hypothesis, we reviewed over 100 relevant studies in the human neuroimaging and neuropsychological literatures and coded them relative to 11 variables, some of which characterized our hypothesis and some of which characterized the previous dichotomies. The results of forward stepwise logistic regressions supported our characterization of the 2 systems and showed that this model predicted the empirical findings better than either the traditional dichotomies or a left–right difference.

Keywords: cortical function, dissociation, neuroimaging, neuropsychology, meta-analysis

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When one looks at a plastic model of a human brain, one cannot help but immediately notice that the brain is split into two hemispheres—and one cannot help but wonder what the separate cerebral hemispheres do. About 150 years ago, scientists (Broca, 1861; Dax, 1865) reported the first evidence that the left cerebral hemisphere is dominant for language. A growing number of studies have since characterized hemispheric asymmetry by providing an increasing number of functional dichotomies between the two hemispheres. The left hemisphere is conceived of as specialized for language, mathematics, analytic processing, logical thought, temporal and sequential analysis, and serial processing of sensorial information, whereas the right hemisphere is conceived of as specialized for emotional expression, intuition, the recognition of faces and their emotions, artistic achievement, attention, recognition of musical sequences and other musical aptitudes, visuospatial analysis, and parallel processing of sensory information (for reviews see Bradshaw & Nettleton, 1981; Bryden, 1982; Corballis, 1983; Hellige, 1993). Such reports have led to broad dichotomies to account for hemispheric differences—such as that the left is verbal, the right perceptual; the left is logical, the right intuitive; the left is rule bound, the right creative. Ultimately, such oversimplified views of hemispheric specializations led to the concept that individuals have left- or right-hemisphere personalities (see Efron, 1990).

However, two problems challenge such generalizations. First, many findings have turned out to be difficult to replicate. For example, the left hemisphere specialization for verbal processing was first systematically documented in a dichotic listening task (Kimura, 1961). In this paradigm, two different lists of numbers are presented simultaneously, one to the right ear and one to the left ear; because the right ear projects information primarily to the left hemisphere, and vice versa for the left ear, researchers can use differences in left- versus right-ear performance to assess how function is lateralized. However, a right-ear/left-hemisphere superiority for speech signals is statistically significant in less than 50% of the entire population (see Speaks, Niccum, & Carney, 1982).

Second, there are many exceptions to the generalizations. For example, for verbal ability, the left hemisphere is better at using the rules of grammar, whereas the right is better at understanding metaphors (Brownell, Simpson, Bihrle, Potter, & Gardner, 1990). Similarly, for perceptual ability, the left hemisphere is better at categorizing spatial relations (such as that one object is left of another), whereas the right is better at specifying precise distances (such as between two objects; Kosslyn, 2006). In short, one could argue that for the most part, the left and right halves of the brain may be more like the kidneys or the lungs: There are two of them, but they are redundant. In some respects the hemispheres are different, but most of those differences appear to be quantitative (e.g., affecting the amount of time required to perform a task), not qualitative.

Another anatomical distinction offers a more promising way to organize human cortical function at a macrolevel, namely between the cortical areas roughly located above the Sylvian fissure and the cortical areas located below it (e.g., Blazhenkova & Kozhevnikov, 2009; Kozhevnikov, Kosslyn, & Shephard, 2005). Traditionally, the two regions are characterized as a dorsal (top) system that processes information about spatial characteristics of objects, such as location and movement (i.e., a "where" pathway), and a ventral (bottom) system that processes information about object features, such as shape and color (i.e., a "what" pathway; Ungerleider & Mishkin, 1982). The dorsal system has also been characterized as a "how" system, where visuospatial information is processed by the motor system to guide action (Goodale & Milner, 1992).

Although converging evidence from neuropsychological and neuroimaging data documents a robust functional dissociation between the two systems, the functions attributed to the two pathways have not yet been systematically characterized. In this article, we propose a more detailed characterization of the functions carried out by the dorsal and ventral cortical areas of the human brain. To evaluate this proposal, we conducted a meta-analysis of relevant neuroimaging and neuropsychological findings.

In what follows, we first briefly review key findings in the literature that characterize the dorsal and ventral systems; then we turn to our hypothesized information-processing characterization of the two systems; and then we report our meta-analysis of relevant findings.

Evidence for the Dorsal–Ventral Distinction

Evidence for the dissociation of processing in the two cortical systems comes primarily from studies of behavioral deficits following damage to the one or the other system and from neuroimaging studies.

Studies of Behavioral Deficits Following Brain Damage

Pohl (1973) reported what was probably the first systematic empirical evidence that the ventral and dorsal systems have distinct functions in primates. This work was followed up and expanded by Ungerleider and Mishkin (1982), whose article had a massive influence (as of this writing, that article has been cited in over 3,100 published works). They trained monkeys in an object-discrimination task and showed that lesions of the inferotemporal cortex (part of the ventral system) not only disrupted memories but also devastated the animals' ability to relearn the discriminations. In sharp contrast, these lesions had very little effect on the animals' ability to discriminate between spatial locations. However, lesions of the parietal lobes had the reverse effect, devastating the spatial task but barely affecting the object-discrimination task. These results led Ungerleider and Mishkin to suggest that the ventral pathway, running from occipital cortex down to the inferotemporal cortex, is responsible for the visual identification of objects and the processing of object properties (such as color, size, and texture), whereas the dorsal pathway, running from occipital cortex up to the posterior parietal cortex, is responsible for the perception of spatial relations and processing of spatial properties of objects (such as their orientation and location).

In the years since this landmark study, researchers have shown that this dissociation extends beyond the posterior parts of the monkey brain. For example, Wilson, Scalaidhe, and Goldman-Rakic (1993) showed that the ventral pathway projects to the ventrolateral prefrontal cortex, whereas the dorsal pathway projects to the dorsolateral prefrontal cortex, mediating, respectively, object working memory and spatial working memory.

In addition, studies of human patients with brain damage (e.g., Levine, Warach, & Farah, 1985; Newcombe, Ratcliff, & Damasio, 1987) have documented a comparable organization of the human brain into ventral and dorsal pathways. However, on the basis of studies of humans with brain damage, Goodale and Milner (1992) proposed an alternative account of the functions carried out by the two cortical pathways. Within their framework, the dorsal pathway mediates the control of action by transforming spatial information about objects (locations and spatial configurations) to guide actions. In contrast, the ventral pathway identifies objects, actions, and causal relations between them (see also Milner & Goodale, 1995; Goodale, 2008). This characterization led Goodale and Milner to dub the dorsal and ventral pathways the *how* and *what* systems, respectively.

Goodale and Milner (1992) marshaled various sorts of evidence to support their characterization. For example, patients suffering from Bálint's syndrome (which involves lesions of the superior posterior parietal cortex, part of the dorsal pathway) have problems reaching toward targets, especially when the targets are located in the periphery of their visual field, but they have relatively spared abilities to recognize objects and to remember locations in space (e.g., Perenin & Vighetto, 1988). The opposite pattern of deficits has been reported for patients with ventral pathway lesions (e.g., Goodale, Milner, Jakobson, & Carey, 1991). However, other researchers (e.g., Laeng, 1994) showed that patients with damage to the posterior parietal lobe have difficulty with spatial relations even when they are not used to guide or

monitor movements; thus, the dorsal pathway must be doing more than processing motor-based information.

Neuroimaging Studies

Such neuropsychological findings, based on behavioral deficits following brain damage, have been augmented by results from neuroimaging studies (e.g., Haxby et al., 1991). These results have both documented the distinction between the two systems and challenged current characterizations of their functions. For example, Konen and Kastner (2008) found that processing information about objects is not restricted to the ventral system but can also be observed in several cortical areas in the dorsal system. In addition, researchers have shown that the anatomical and functional dissociation between the two systems is not restricted to the visual modality. For instance, Hickok and Poeppel (2004, 2007) have proposed a similar dual pathway model for auditory language processing. From the superior temporal gyrus engaged in early stages of speech perception a dorsal pathway projects to the inferior parietal and posterior frontal regions and mediates auditory–motor integration, whereas a ventral pathway projects to the middle and inferior temporal cortices and processes the meaning of sounds.

Characterizing the Two Systems: A New Hypothesis

Although ample evidence indicates that the dorsal and ventral systems are distinct, the functions attributed, respectively, to the dorsal (i.e., parietal cortex and dorsal frontal cortex) and the ventral (i.e., occipital, temporal, and orbitofrontal cortices) cortical areas of the human brain have not been characterized in detail. Rather than simply specifying dichotomies, we consider the nature of the *information processing systems* each area implements. To begin, we assume that the same principles apply to both visual and auditory information. We argue that the full dorsal system (including the relevant frontal cortices) is *expectation driven*. That is, this system generates predictions, and processing largely rests on evaluating the expectations that arise from such predictions. To evaluate expectations, the system must (a) process sensory information arriving in sequence, over time; (b) organize such information by producing representations of spatial or temporal relations between multiple objects, points, or fragments of information; (c) register movement, which is indicated by changes over time in the spatial properties of an individual object; and (d) guide and track movements by encoding changes in spatial relations between two or more objects (e.g., between the hand and a desired object).

In contrast, we hypothesize that the full ventral system (including portions of orbital and ventral medial frontal cortex) is *classification driven*. That is, this system classifies perceived stimuli, and processing largely rests on identifying input. To classify stimuli, the system (a) must evaluate input using parallel processing (otherwise it would be too slow, when comparing input to a large number of stored memories); (b) must consider each object separately

(although other individual objects can prime or otherwise influence such processing, via feedback loops; cf. Ganis & Kosslyn, 2007); (c) must focus on shape and other object properties (such as color and texture for visual input, and frequency and amplitude for auditory input), not on movement per se; and (d) would not be used in motor control per se but rather would process information about objects that are the targets of guided movements the same way it processes objects that are not targets.

Meta-Analysis

We evaluated our proposed information-processing characterizations by using a logistic regression meta-analysis of the neuroimaging and neuropsychology literature. Our search of the literature was driven by (a) the domain of the functions attributed to the dorsal and the ventral pathways in the standard w*hat versus where* and w*hat versus how* dichotomies and (b) the types of information processing we hypothesized to occur in the expectation-driven and the classification-driven systems, which also address that domain. To expand beyond this domain (for example, by considering emotion) would be inappropriate, at least in a first attempt to characterize the nature of information processing in the dorsal and ventral systems—the classical dichotomies were never intended to apply to such types of phenomena. We do not intend to minimize the importance of additional functions of the systems but rather wish to revisit the standard dichotomies and to demonstrate that the classical functions attributed to the dorsal and ventral systems of the human brain are inadequate because they do not rely on precise characterizations of the information processing that takes place in the two systems.

After having identified all relevant research reports, we coded the nature of the task for each study, noting the value of a set of specific variables; in addition, we coded the results of each of the studies, noting whether each reported a deficit or deficits following damage to one or the other cortical region (for neuropsychological studies) or whether activation occurred in one or the other cortical region (for neuroimaging studies). Finally, we carried out a series of logistic regression analyses on these codings to determine which variables affect the functioning of the two systems.

In the following sections, we describe how we selected results to be analyzed; we then describe how we analyzed them and what we found.

Inclusion Criteria and Selection of Studies

Our inclusion criteria for the meta-analysis were as follows: (a) We included only neuroimaging studies that relied on positron emission tomography (PET) or functional magnetic resonance imagery (fMRI). (b) We included cortical lesion studies when the lesions involved were discrete and individual lesions did not overlap the dorsal and ventral portions of the cortex; and we included selected transcranial magnetic stimulation (TMS) studies, as a transient lesion technique used with normal participants. (c) Studies had to focus only on cortical (not subcortical) brain areas.

(d) Neuroimaging studies had to include a baseline condition, and we included only the analysis of the brain areas activated when an experimental condition was contrasted to a baseline condition. (e) Studies were included only if enough details were provided to allow us to code the variables we used; thus, findings summarized in short reports or in parts of a review typically were not included.

With these requirements in mind, we used the PubMed database to search for relevant articles. The search terms we used were dictated by information-processing functions, not by cortical areas. We began by including terms that capture the classical functions purported to be computed by the ventral and the dorsal systems because we needed to compare our model with the traditional what–where and what–how dichotomies. We also included terms that addressed variables that should be important if the present information-processing hypothesis is correct. Specifically, the search keywords we used were as follows: *parallel processing, serial processing, sequential processing, action planning, sequence preparation, motion processing, shape processing, object processing, object identification, object recognition, spatial relations, temporal relations, what–where, object–spatial, auditory relations representations, music relations,* and *music structure.* In addition, we included search terms for the methodologies of interest: *fMRI, TMS, PET, neuropsychology,* and *brain lesions.* We restricted this search to data on humans. Using this search procedure, we identified 140 references—all journal articles from 1987 through January 2010. A total of 77 studies of the original 140 met the aforementioned criteria (see Supplemental Materials for a list of the references in the meta-analysis). Many of these reports included multiple experiments. Thus, each qualifying experiment was included in the meta-analysis and counted as a single case. There was a total of 107 cases across the 77 studies (see Table 1 for a summary of the characteristics of the 107 cases).

Variable Selection, Coding, and Reliability

We first identified 11 independent variables that reflected the functions we, or others, hypothesized to characterize the two systems. We identified variables that represent both the classic functional dichotomies (i.e.,

where versus what and how versus what) and the functions specified by our new characterization. Thus, the variables were as follows: (a) classification, (b) shape processing, (c) color processing, (d) texture processing, (e) explicit shape organization, (f) parallel processing, (g) spatial relations, (h) conceptual relations, (i) sequencing, (j) top-down processing, and (k) movement. In addition, for each experiment, we coded the location of the lesion (for lesion studies) or location of activation (for neuroimaging studies) using six dependent variables that specified anatomical dissociations along the three main axes in the brain (top–bottom, front–back, and left–right).

For each independent variable we coded 1 if the experimental task featured the property and 0 if it did not. We created four dummy variables to represent the two classical functional dichotomies. To represent the *where versus what* dichotomy, for *where* we coded 1 if the task was visual *and* spatial relations processing had been coded 1. For *what* we coded 1 for that case if the task was visual *and* shape processing, color processing, or texture processing had been coded 1. To represent the *how versus what* dichotomy, for *how* we coded 1 if the task featured spatial relations processing *and* movement. For *what* we coded 1 if the task had been coded 1 on shape processing, color processing, or texture processing. In addition, for tasks that required identification of an action, we also coded 1 on the what variable of the *how versus what* dichotomy.

For each dependent variable, we coded 1 if the area (i.e., top, bottom, left, right, front or back) of the cortex was damaged or activated (for lesion and neuroimaging studies, respectively) and 0 if not. For neuroimaging studies, we coded dorsal activation as 1 if activation was observed in the parietal cortex and the dorsal areas of the frontal lobes (i.e., Brodmann Areas 1 to 9, 39, 40, 46). We coded ventral activation as 1 if activation occurred in the occipital, temporal, and/or orbitofrontal cortices (i.e., Brodmann Areas 20, 21, 37, 10–14, and 47). We coded front activation as 1 when activation anterior to the central sulcus was observed; if activation posterior to the central sulcus was observed, we coded 1 for back activation. We note that the codings were not mutually exclusive; thus, for a given study, multiple independent and dependent variables could be coded 1.

Two of the authors (Grégoire Borst and William L. Thompson) independently coded the studies. Reliability for the individual independent variables ranged from 79% to 99%, and reliability for the individual dependent variables ranged from 88% to 91%. Overall mean reliability was 93% for the independent variables and 90% for the dependent variables. When the codings were different, a brief discussion always produced a consensus for the appropriate coding.

Logistic Regression Analysis

The logic of the logistic regression analysis is as follows: If the cerebral cortex is organized into separate dorsal and ventral systems, different variables (reflecting different types of information processing) should predict the behavioral deficits following damage to, or activation of, the top

Table 1
Summary of the Type of Stimuli for Different Methods Used in the 107 Cases Included in the Meta-Analysis

Stimulus type	fMRI	PET	TMS	Lesions	Total
Visual	49	7	0	30	86
Auditory	10	0	2	2	14
Both visual and auditory	6	0	0	1	7
Total	65	7	2	33	107

Note. fMRI = functional magnetic resonance imaging; PET = positron emission tomography; TMS = transcranial magnetic stimulation.

and bottom areas of the cortex. Moreover, we reasoned that if the functional dissociation goes beyond the standard *where versus what* and *how versus what* dichotomies, other variables—which reflect additional aspects of information processing (such as processing of sequences or categorization of stimuli into a specific class)—should predict damage or activation, even after controlling for the variables associated with the standard dichotomies.

For each dependent variable, we conducted a stepwise binary logistic regression analysis; logistic regression was necessary because the dependent variables were coded 1/0. Before conducting these analyses, we removed any independent variable with fewer than 12 cases that were coded with a value of 1. Thus, the variables texture, explicit shape organization, and conceptual relations were not included in the logistic regression analyses. Our removing these variables did not lead us to discard any study because the 21 cases coded as 1 on these variables were also coded as 1 on other independent variables.

We entered all independent variables in two separate stepwise logistic regressions, one for the dorsal-related and one for the ventral-related dependent variables. As shown in Table 2 (section A), four variables predicted the probability that the dorsal areas of the cortex were involved in a task (either damaged or activated, depending on the nature of the study), namely shape processing, spatial relations, sequencing, and movement. Shape processing had a negative regression coefficient, which suggests that performing a task where a shape had to be processed decreased the probability of observing behavioral deficits following lesions or activation in cortical areas located in the dorsal portion of the brain.

In contrast, three variables predicted the probability that the ventral cortical areas of the brain were involved in a task (either damaged or activated, depending on the nature of the study): parallel processing, spatial relations, and sequencing. Both spatial-relations processing and se-

quencing had negative logistic regression coefficients, which indicates that bottom cortical areas play a specific role in parallel processing.

Contrary to our prediction, classification was not one of the variables that predicted the probability of behavioral deficits or activation of the ventral system. One possible explanation is that some of the experiments that required classification required specifically spatial categorization, which may rely as much on dorsal as on ventral cortical areas. To evaluate this hypothesis, we removed these experiments from the logistic regression analysis (which left us with a total of 89 cases) and repeated the analyses. As shown in Table 2 (section B), we now found that sequencing and movement predicted behavioral deficits or activation of the dorsal cortical areas, whereas classification was the critical variable that predicted behavioral deficits or activation in the ventral cortical areas of the brain.

However, one could argue that the functional dissociation along the top–bottom divide actually reflects front–back or left–right functional dissociations. For example, perhaps most of the dorsal deficits followed from damage to, and activation occurred in, the left frontal regions—and it was either the left hemisphere or frontal location that was driving the results. To control for this possibility, we conducted additional stepwise logistic regressions where we forced into the logistic regression model the front, back, left, and right codings and then entered all 11 independent variables. As evident in Table 3, after factoring out the contributions of front versus back and left versus right dimensions, we found that dorsal cortical areas mediate spatial relations processing, sequence processing, and movement processing, whereas ventral cortical areas are specifically involved in classification. Thus, the functional dissociation along the top–bottom divide exists independently of any functional dissociation between left–right or front–back cortical areas.

Table 2
Results of the Stepwise Logistic Regressions When (A) All Cases Are Included in the Analysis and (B) the Analysis Is Restricted to Cases Without Spatial Categorization

Variable	(A) All cases						(B) Cases minus spatial categorization cases					
	Top			Bottom			Top			Bottom		
	B	Wald	p	B	Wald	p	B	Wald	p	B	Wald	p
Classification										1.60	4.16	.04
Shape	−1.72	9.95	.001				−2.18	12.25	.001			
Color												
Parallel processing				1.47	7.92	.001						
Spatial relations	1.58	7.91	.001	−1.17	4.84	.03				−1.51	4.02	.05
Sequences	2.90	7.03	.01	−2.42	14.98	.001	3.00	7.02	.01	−3.04	15.37	.001
Top–down												
Movement	1.99	6.58	.01				2.56	10.24	.001			
Constant	0.21	0.21	.64	0.73	1.87	.17	0.48	1.29	.26	1.13	3.93	.05

Table 3

Results of the Stepwise Logistic Regressions When the Front–Back and the Left–Right Divides Are Controlled for, by Initially Forcing Them Into the Logistic Regression Model

Variable	Top B	Top Wald	Top p	Bottom B	Bottom Wald	Bottom p
Front	1.00	1.85	.17	0.52	0.57	.45
Back	0.40	0.15	.70	2.04	3.77	.05
Left	0.76	1.24	.27	0.33	0.23	.63
Right	0.28	0.17	.68	1.43	4.00	.05
Classification				1.92	10.98	.001
Shape	−1.38	5.09	.02			
Color						
Parallel processing						
Spatial relations	1.88	9.02	.001	−1.71	8.49	.001
Sequences	2.60	5.37	.02	−2.35	9.67	.001
Top–down						
Movement	1.99	6.18	.01			
Constant	−1.56	1.34	.25	−2.48	2.87	.09

We next examined fine-grained functional dissociations in the cortex by combining the top versus bottom and front versus back divides (i.e., examining separately top–front, top–back, bottom–front, and bottom–back regions). As shown in Table 4, logistic regressions revealed that the top–front cortical areas mediate sequencing of sensory information, the top–back cortical areas process spatial relations and movement, whereas the bottom–back cortical areas are activated when parallel processing is needed. No variables were associated with anterior parts of the temporal lobe.

All of these fine-grained functional divides are consistent with functions classically attributed to the front (i.e., sequences in the frontal lobe) and back (spatial relations and movement in the parietal and motor cortices) cortical areas of the brain. This is an important finding because it validates the sample of studies chosen by showing that the findings are consistent with those from previous studies and provides evidence that our sample was large enough to find systematic relationships with multiple variables. For example, studies have documented the role of the prefrontal cortical areas in processing sequences by showing that neurons in prefrontal cortex respond specifically to the sequential positions of a stimulus within an ordered series (e.g., Barone & Joseph, 1989). The prefrontal cortex also mediates planning—such as in the Tower of London task (e.g., Owen, Downes, Sahakian, Polkey, & Robbins, 1990; Shallice 1982, 1988)—and codes serial order of information (e.g., Amiez & Petrides, 2007; Averbeck & Lee, 2007).

Table 4

Results of the Stepwise Logistic Regressions When the Top–Bottom and the Front–Back Divides Are Combined, Resulting in the Characterization of Activation Into Quadrants

Variable	Top–Front B	Top–Front Wald	Top–Front p	Top–Back B	Top–Back Wald	Top–Back p	Bottom–Front B	Bottom–Front Wald	Bottom–Front p	Bottom–Back B	Bottom–Back Wald	Bottom–Back p
Classification												
Shape	−1.62	9.43	.001									
Color	−20.3	0.001	1.00									
Parallel processing										1.33	8.10	.001
Spatial relations				1.50	10.69	.001						
Sequences	1.49	7.59	.01							−1.93	11.26	.001
Top–down												
Movement				1.47	6.63	.01						
Constant	−0.41	1.31	.25	−0.73	6.72	.01	0.28	2.09	.15	−0.09	0.05	.82

Another way to test the information-processing characterizations we propose is to identify the variables that predict the data after the influence of the where–what (e.g., Ungerleider and Mishkin, 1982) or the how–what (e.g., Milner & Goodale, 1995) variables are removed. To this end, we conducted four stepwise logistic regressions in which we forced the where–what or how–what variables into the model before we entered the other independent variables. Crucially, as shown in Table 5, even after the influence of the where–what variables was removed, the requirements of processing sequences and movement predicted the probability of deficits following, or activation of, the dorsal cortical areas, whereas classification predicted the probability of deficits following damage to, or activation of, the ventral cortical areas. As shown in Table 6, we found that the dorsal areas of the cortex mediate spatial relations, sequences, and movement processing, whereas the ventral areas mediate classification after the contribution of the how–what variables was removed. Thus, without question, our characterization of the functional organization of the cortex encompasses and further extends the previous dichotomies.

Discussion

The functions of the dorsal and ventral systems are better explained by an information-processing approach than by the standard *where versus what* or *how versus what* dichotomies. As predicted by the idea that the dorsal system is expectation driven, we found evidence that this system processes sequences of sensory information, relations between different sets of information, and actions. And as predicted by the idea that the ventral system is classification driven, we found evidence that this system engages in parallel processing, categorizes sensory information, and processes properties of objects (such as color and shape). Moreover, we found that the human dorsal system is not restricted to the posterior parietal lobe but also includes the premotor areas, the frontal eye fields, and the dorsolateral prefrontal cortex; in addition, the human ventral system is not restricted to the infrotemporal cortex but also includes the orbitofrontal cortex.

Given that our analyses included both visual and auditory studies, one could argue that our results generalize over both types of studies. However, it is possible that the findings are in fact driven by one type, with the other showing no effect. Thus, to make the case that the findings do generalize over modality, we must show that the dissociation between the expectation-driven and the classification-driven systems applies to vision and audition considered separately. Therefore, we conducted additional logistic regression analyses of only the visual studies (89 cases), which produced the same pattern of results that we found with the entire sample of studies (107 cases). This finding demonstrated that the dissociation does indeed apply to the processing of visual information. However, we could not conduct the corresponding analysis of only the auditory data because we did not have enough studies in our sample (14). To provide evidence that the dissociation applies to auditory processing per se, future meta-analyses will need to include a larger sample of auditory studies.

In addition, we found that some of the functions mediated by the dorsal and ventral systems also rely on the front or back portions of the cortex. For example, we found that sequences are processed in the top–front cortical areas, whereas parallel processing is essentially related to bottom–back areas of the cortex. These results document that the sample of studies used in our meta-analysis was not simply driven by our own hypotheses, given that the functions we identified as mediated by the front portion of the cerebral cortex, for example, have previously been associated with these areas.

Two criticisms could be raised regarding the present project—one regarding the pertinence and the timeliness of the goals and one regarding the methodology adopted. First, a critic could question whether the goals of the present project make sense in view of recent findings on cortical function. Contemporary studies in cognitive neuroscience have converged on the idea that the brain is best

Table 5

Results of the Stepwise Logistic Regressions When the Variables Associated With Where–What Functions Are Controlled for, by Forcing Them Into the Model

Variable	Top			Bottom		
	B	Wald	p	B	Wald	p
What	−2.15	13.67	.001	1.29	5.61	.02
Where	1.62	6.82	.01	−1.27	4.38	.04
Classification				1.52	7.85	.01
Parallel processing						
Spatial relations						
Sequences	2.98	7.28	.01	−2.07	11.25	.001
Top–down						
Movement	2.16	7.93	.005			
Constant	0.65	1.94	.16	−0.06	0.02	.89

Table 6
Results of the Stepwise Logistic Regressions When the Variables Associated With How–What Functions Are Controlled for, by Forcing Them Into the Model

Variable	Top			Bottom		
	B	Wald	p	B	Wald	p
What	−1.78	9.47	.01	1.04	3.64	.06
How	17.66	0.00	1.00	0.05	0.00	.95
Classification				1.31	5.27	.02
Parallel processing						
Spatial relations	1.48	6.70	.01	−1.44	6.68	.01
Sequences	2.95	7.13	.01	−2.14	11.20	.001
Top–down						
Movement	1.73	4.55	.03			
Constant	0.36	0.53	.47	0.46	0.71	.40

conceived of as a set of overlapping, distributed neural networks (e.g., Nobre, Gitelman, Dias, & Mesulam, 2000). Given this idea, should we be trying to characterize what the different parts of the brain do? We have three responses to this concern: First, these distributed networks are networks among specific brain areas—and different brain areas do different (sometimes very complex) things. To understand in detail what the networks do, we need to describe both the functions of individual brain areas and the ways in which these areas interact. We stress that we cannot describe how brain areas work together as a distributed network unless we have some idea of what they do. Second, we conceive of the two large systems—dorsal and ventral—as separate networks, which is directly supported by the neuroanatomy: There is no doubt that the dorsal and ventral systems are distinct networks of cortical areas. Third, our approach, which is based on characterizing information-processing systems, allows us to explain why different tasks activate partially overlapping sets of brain areas, which is not possible when the brain's macrolevel organization is expressed in terms of dichotomies.

The second criticism is that one shortcoming of our meta-analysis is that we coded the damage to, or activation of, the cortex as 1 or 0—with no gradation of the severity of the lesion or the magnitude of the blood-oxygen-level-dependent (BOLD) signal—which forced the type of logistic regression analysis we used (i.e., binary logistic regression). One could wonder whether the results of our meta-analysis are a consequence of our binary coding. However, we note that because our codings were not mutually exclusive—the behavioral impairment following brain damage or activation could be coded 1 for dorsal and 1 for ventral cortical areas—it is unlikely that the binary coding can explain our findings.

By characterizing more precisely the nature of information processing in the ventral network and the dorsal network, we can account for a broader number of neurocognitive results than are subsumed by the classical dichotomies—even some results that first appear to contradict the dichotomies. For example, Konen and Kastner (2008) found object-selective responses in areas along both the ventral and the dorsal pathways. Critically, all stimuli (2D, 3D, and line drawings of objects) activated the human posterior parietal cortex (PPC) even though stimuli were presented at the same location and most of them were not associated with actions. The activation of the PPC by such stimuli would not be predicted by either the where–what or the how–what dichotomies. However, given that stimuli were presented sequentially over time, such activation of the dorsal areas of the cortex is just as expected by our model.

In conclusion, our analyses clearly show that an information-processing approach allows us to characterize the ventral–dorsal distinction better than simple dichotomy-based approaches do. Moreover, our analyses revealed that the two large systems themselves must be decomposed further, for example into their anterior and posterior portions. Extending the meta-analysis to the literature on the functions carried out by the anterior versus the posterior areas of the cortex and combining it with the analysis on the dorsal–ventral divide should make it possible to devise a detailed model of the macrolevel organization of the human cerebral cortex.

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For a complete list of the studies in the meta-analysis, go to http://dx.doi.org/10.1037/a0024038.supp

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