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Neural substrates of processing path and manner information of a moving event

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Abstract

Languages consistently distinguish the path and the manner of a moving event in different constituents, even if the specific constituents themselves vary across languages. Children also learn to categorize moving events according to their path and manner at different ages. Motivated by these linguistic and developmental observations, we employed fMRI to test the hypothesis that perception of and attention to path and manner of motion is segregated neurally. Moreover, we hypothesize that such segregation respects the "dorsal-where and ventral-what" organizational principle of vision. Consistent with this proposal, we found that attention to the path of a moving event was associated with greater activity within bilateral inferior/superior parietal lobules and the frontal eye-field, while attention to manner was associated with greater activity within bilateral postero-lateral inferior/middle temporal regions. Our data provide evidence that motion perception, traditionally considered as a dorsal "where" visual attribute, further segregates into dorsal path and ventral manner attributes. This neural segregation of the components of motion, which are linguistically tagged, points to a perceptual counterpart of the functional organization of concepts and language.

Keywords: Categorization; Dorsal visual stream; Functional magnetic resonance imaging (fMRI); Selective attention; Motion; Talmy

What is the relationship between space and language? This question has been of considerable interest to linguists and psychologists in the past decades (Bloom, Peterson, Nadel, & Garrett, 1996; Hayward & Tarr, 1995; Landau & Jackendoff, 1993; Landau & Zukowski, 2003; Tanenhaus, Spivey-Knowlton, Eberhard, & Sedivy, 1995). In these research programs, language, rather than being considered an autonomous cognitive module, is usually conceived of as linked to and constrained by non-linguistic factors. While the precise relationship between perception, conception and language may be "sketchy" (Papafragou, Massey, & Gleitman, 2002), it does not appear to be arbitrary. The linguist Talmy (2000a) suggests that considering the inter-penetrability of perception and conception opens the way to identifying common parameters across cognitive domains that might otherwise remain obscured. In contrast to linguistics and psychology, there has been relatively little interest in the interface of space and language in cognitive neuroscience (but see Chatterjee, 2001; Kemmerer, 2006). In keeping with the spirit of Talmy's suggestion, we investigate whether the linguistic parsing of space is paralleled by a neural decomposition of spatial events.

Spatial representations can be conceptualized in many ways. These include representations involving imagery, navigation, and reaching and grasping behaviors. However, "thinking for speaking" is likely to be different from thinking for other purposes (Slobin, 1996). In this study, we focus on components of spatial representations as events directly relevant to language. Specifically, we focus on the path and the manner of motion embedded within a dynamic event. Path refers to the trajectory of a moving figure with respect to its background or to an orienting point. Manner refers to the way in which a figure moves intrinsically regardless of its trajectory. Although a moving event usually involves a specific combination of path and manner, these two kinds of motion information are segregated when

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mapped on to language (Talmy, 1985). For example, in English manner of motion is expressed most often by the main verb of a sentence (e.g., *run, walk*) and path of motion is expressed most often by the prepositional phrase (e.g., *along* the road, *into* the house). Talmy (2000b) described such "characteristic expression of motion" as "colloquial rather than literary", "frequent rather than occasional", and "pervasive rather than limited". However, Talmy also noted that the relationship between the semantic elements and the surface linguistic forms is "largely not one-to-one". In other words, the characteristic expression is not the only linguistic pattern to convey a particular semantic domain (Talmy, 2000b).

Not all languages follow the same mapping of motion components to language constituents as English. Following Talmy's binary typology (1985, 2000a, 2000b), most languages in the world express the path of motion either by the main verb (verb-framed) or by a satellite to the main verb (satellite-framed). Verb-framed languages (e.g., French, Greek, and Spanish) usually express the manner of motion by an adverbial phrase. In contrast, satellite-framed languages (e.g., English and Chinese) usually express the same meaning by the main verb. For example, English and Spanish convey the same event as "The bottle floated into the cave." and "La botella entra en la cueva flotando (*The bottle moved into the cave floating*)", respectively. Although such typology provides a useful framework for identifying the fundamental attributes of motion events, it does not account for the diversity of all different languages. As Slobin (2004) pointed out, for languages with serial verbs (e.g., Sino-Tibetan) and bipartite verbs (e.g., Hokan), it is not always clear which is the main verb and whether it only expresses the path but not the manner of motion. Also, for languages with a manner preverb and a path preverb before the main verb (e.g., Jaminjun), both path and manner are expressed by the same grammatical form (Slobin, 2004). As a result, Slobin proposed a third type of languages, namely, equipollently-framed languages, to account for the languages that do not easily fit the binary typology proposed by Talmy.

Despite these caveats, the cross-linguistic generalization that "path" does not conflate with "manner" into a single verb root seems to capture the "characteristic tendency" (Levinson & Wilkins, 2006) of most languages in the world, even though the accessibility of different linguistic forms, the dynamics of cultural and aesthetic values can influence habitual patterns of language use (Slobin, 2004). It should also be pointed out that path and manner information of a moving event, of course, remains accessible to speakers of different languages (Jackendoff, 1990, 1996) in spite of being expressed by different linguistic constituents across languages. English and Greek speakers perform non-linguistic tasks (i.e., memory and categorization) similarly, even though verbs in the two languages emphasize different motion components (Papafragou et al., 2002). Similarly, native English and Spanish speakers do not differ in their recognition memory of moving events (Gennari, Sloman, Malt, & Fitch, 2002). For our purpose, the important point is that most languages segregate path and manner components of dynamic spatial events into distinct linguistic constituents. This functional linguistic segregation raises the question of whether the nervous system also segregates path and manner when processing dynamic spatial events.

A dominant theory of vision is that visual information is processed within two visual streams that are specialized for processing "what" and "where" information, respectively (Ungerleider & Mishkin, 1982). The "what" pathway involves the ventral regions important for visual recognition. The "where" pathway involves the dorsal regions important for the spatial localization of an object. Perception of motion is consistently ascribed to the dorsal stream based on evidence from both monkeys and humans (e.g., DeYoe & Van Essen, 1988; Heeger, Boynton, Demb, Seidemann, & Newsome, 1999; Lewis, Beauchamp, & DeYoe, 2000; Orban et al., 1995; Tootell et al., 1995; Zeki et al., 1991). Specifically, the middle temporal visual area in macaques (MT/MST) and an analogous area in humans, found most often within the junction of the inferior temporal gyrus and the occipital cortex, respond to motion stimuli and in tasks requiring motion discrimination.

Much previous research on visual motion processing has focused on movements of simple stimuli. For example, Beauchamp, Cox, and DeYoe (1997) presented to participants moving dots toward different directions with different colors. They identified brain regions that were selectively responsive to motion but not to color in MT/MST and the parietal lobule. They also found that the activation within these regions was modulated both by spatial (at the center vs. periphery of the visual display) and featural (motion vs. color) attention to the stimulus. Seiffert, Somers, Dale, and Tootell (2003) also employed simple visual displays (e.g., sine-wave radial gratings, concentric rings with sinusoidal contrast modulation) to determine whether the texture, luminance, and attention of moving stimuli was associated with distinct neural substrates. They found no differences between the processing of these aspects of movements.

Recently, the neural basis of more complex motion has been investigated. Most notably, both banks of the superior temporal sulcus are implicated in biological motion (Allison, Puce, & McCarthy, 2000; Decety & Grezes, 1999; Grossman et al., 2000) and action events (Kable & Chatterjee, 2006), which may be distinguished from mechanical motion (Martin & Weisberg, 2003). The extrastriate body area (EBA; Downing, Jiang, Shuman, & Kanwisher, 2001) and the fusiform body area (FBA; Peelen & Downing, 2005) also demonstrated preferential activation to biological motion (Peelen, Wiggett, & Downing, 2006). Furthermore, human MT/MST is even sensitive to implied (as opposed to actual) motion as evidenced by the response to pictures of actions, even when the pictures themselves are static (Kable, Spellmeyer-Lease, & Chatterjee, 2002; Kourtzi & Kanwisher, 2000). These observations suggest that specific regions of the nervous system specialize in processing different aspects of motion. However, the possible components of motion probed thus far has not been motivated directly by the functional organization of language.

In the current study, we employed fMRI to investigate whether attention to the path or manner of motion activates different neural networks. For two reasons we predicted that path would be processed more dorsally than manner, despite motion itself being generally subsumed under the dorsal visual processing stream. First, path information conveys a trajectory that almost any object can traverse in space, whereas manner information conveys the kind of motion constrained by bio-mechanical properties of the object itself. For example, a horse and a turtle can both walk, but only the horse can gallop, and a ball can neither walk nor gallop. However, all three can move across a field or into a garden. Since path is about "where" an object is moving in space while manner is about "what" kind of movement an object is possible of doing, path should be processed more dorsally than manner if the where/what-dorsal/ventral mapping observed in the visual domain is a general principle of neural organization. Second, we previously found that verb processing activates the posterior middle temporal gyrus (Kable et al., 2002; Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005) and others have implicated the posterior inferior parietal cortex in processing prepositions (Damasio et al., 2001; Emmorey et al., 2002; Kemmerer, 2006). If language and perception are indeed linked anatomically and in English manner is conveyed by verbs and path by prepositional phrases, then we would also predict a dorsal–ventral organization for processing path and manner of motion. We should be clear that we are not testing a hypothesis about the properties of language, per se, in this study. Rather we are testing a hypothesis about perception, which is motivated directly by properties of language. The hypothesis, if confirmed, would suggest that the neural organization of perception parallels (and possibly undergirds) the functional organization of language.

1. Experiment 1

In this experiment, we tested the hypothesis that processing of path and manner of motion is associated with distinct neural substrates. We predict that the sub-divisions within motion processing would respect the ventral-what and dorsal-where organization of the visual system.

1.1. Methods

1.1.1. Participants

Eight volunteers (four men and four women) from the community of University of Pennsylvania participated in this experiment. They were all native speakers of English with normal or corrected-to-normal vision. None of them had a history of neurological or psychiatric disorder. All participants gave informed consent in accordance with the procedures of the Institutional Review Board of University of Pennsylvania.

1.1.2. Materials and design

Three types of short movie clips (i.e., Path, Manner, and Identity) of an animated starfish were created using the software Strata (www.strata.com). The starfish had eyes at the center with five limbs, which resembled a star-like cartoon figure with a face. Each movie consisted of 30 frames per second and lasted 3 s. In each of the 18 movies used in the Path condition, a purple starfish moved along a distinct path within a rectangular frame of 683 × 450 pixels. In each of the 18 movies for the Manner condition, the purple starfish performed a distinct manner of motion, none of which were easily verbalized, while the center of the starfish remained at the center of the frame. In each of the 18 movies for the Identity condition, a stationary starfish with a unique color and pattern was presented. Each stimulus was presented twice to the participants in a scan. Each participant received three scans that were composed of the same stimuli (but in different pseudo-randomized orders) of the three conditions, so that in each scan half of the stimuli shared the same feature (the path, the manner, or the color/pattern) as the previous one, while the other half did not.

1.1.3. Procedures

A one-back task in a blocked design was employed. Specifically, in the Path condition the participants had to judge whether the starfish in the current movie moved along the same path as that in the previous movie. Similarly, in the Manner condition the participants had to judge whether the starfish in the current movie performed the same manner of motion as that in the previous movie. In the Identity condition, the participants simply determined whether the current stationary starfish was identical to the previous one.

The trials were organized into 18 blocks in each of the Path, Manner, and Identity conditions. These blocks were further divided into three scans, with six blocks of each condition in each scan. The order of the different conditions within a scan was pseudo-randomized every three blocks, and independently determined for each participant. Every block lasted 21 s. Each block started with a 3-s indication of the condition, followed by six consecutive movies in that condition. The participants were instructed to perform the one-back task according to the indicated dimension to every stimulus, except the first one in a block, by making a key-press response. The correct answer to half of the trials was "same" while to the other half of the trials was "different". The delivery of the stimulus and the recording of the responses were controlled using the software E-Prime (www.pstnet.com/products/e-prime/) on a personal computer.

1.1.4. Imaging procedures

The participants were familiarized with the task in the three conditions before the scanning session. During the scanning session, the participants lay supine in a 3-T Siemens Trio scanner. The stimuli were back-projected onto a screen at the back of the scanner bore and the participants viewed the stimuli through a mirror mounted on the head coil. The manual responses were transmitted using a custom designed fiber-optic response pad. An USA Instruments four-channel head coil was employed to record the fMRI signals. BOLD-sensitive, T2*-weighted functional images were acquired in 3 mm isotropic voxels using a gradient-echo, echoplanar pulse sequence ($\mathrm{TR} = 3000\,\mathrm{ms}$, $\mathrm{TE}_{\mathrm{eff}} = 30\,\mathrm{ms}$). Forty 3-mm slices were acquired during each repetition, with each slice containing a 64 × 64 matrix within a 192 × 192 mm field-of-view. Head motion was minimized using foam padding, and the scanner performed both prospective (3-D Prospective Acquisition Correction, PACE) and retrospective motion correction online. Each participant had three 390-s scans, which contained six blocks of each condition. The participants performed no task during the first 12 s of each functional scan as steady-state magnetization was achieved and these images were discarded. High resolution T1-weighted anatomical images were also acquired for each participant using an MPRAGE pulse sequence ($\mathrm{TR} = 1620\,\mathrm{ms}$, $\mathrm{TE} = 3\,\mathrm{ms}$, $\mathrm{TI} = 950\,\mathrm{ms}$). One hundred sixty 1-mm slices were acquired, with each slice containing a 256 × 256 matrix within a 250 × 250 mm field-of-view.

1.1.5. fMRI data analyses

Functional MRI data processing was performed using VoxBo software (www.voxbo.org) developed at University of Pennsylvania. After image reconstruction, the data were pre-processed in the following steps: First, the data were sinc-interpolated in time slice-by-slice to correct for staggered slice-acquisition (Aguirre, Zarahn, & D'Esposito, 1998). Second, a six-parameter, least-square minimization, motion correction algorithm was applied to realign all function data to the first image acquired for each participant in a scanning session based on that used in the SPM package (www.fil.ion.ucl.ac.uk/spm/). Third, the data were automatically thresholded to exclude extra-parenchymal voxels from subsequent analyses. The scan-wise global signals and power spectra were also derived and stored. Finally, the parameters that permit normalization of the data to a standardized (MNI) space were automatically calculated.

After the pre-processing, six anatomical regions of interest (ROIs) on each hemisphere were drawn on individual participants' images, independent of the functional MRI data. All ROIs were drawn by an experienced neurologist with the aid of a detailed neuroanatomic atlas (Duvernoy, 1999). To determine whether path and manner processing was preferentially associated with certain regions within the dorsal stream, four ROIs covering the dorsal stream along the lateral part of the brain from bottom to top were included: inferior occipito-temporal cortex (Brodmann's area 19 and 37, including visual motion areas, that is, human MT/MST), posterior middle/superior temporal cortex (Brodmann's area 22), inferior parietal lobule (IPL, Brodmann's area 39 and 40), and superior parietal lobule (SPL, Brodmann's area 7). In addition to showing a general

Table 1
The accuracy (%) and reaction time (in ms) in the three conditions of the one-back task from Experiment 1

	Path	Manner	Identity
Accuracy (%)	90	96.9	97.4
Reaction time (ms)	1244	1072	813

sensitivity to motion, we also hypothesize these four regions to demonstrate further dorsal–ventral preference for path and manner processing, respectively. Two ventrally localized ROIs (the parahippocampus and the posterior fusiform gyrus) were also included. The parahippocampal gyrus contains networks sensitive to local visual environments and scenes (Epstein, Graham, & Downing, 2003; Epstein & Kanwisher, 1998). The posterior fusiform gyrus contains networks sensitive to faces and human body parts (Kanwisher, McDermott, & Chun, 1997; Peelen & Downing, 2005).

A voxel-wise analysis within these anatomic ROIs was performed for each participant using a modified version of the general linear model for serially-correlated error terms (Aguirre, Zarahn, & D'Esposito, 1997; Zarahn, Aguirre, & D'Esposito, 1997). This analysis identifies the voxels whose activity was significantly associated with the task covariate (i.e., the two motion conditions in contrast with the Identity condition). The task covariate was a boxcar wave form convolved with an estimate of the BOLD hemodynamic transfer function empirically derived from the motor cortex in a large group of participants (Aguirre et al., 1998). That is, within each anatomical ROI of each participant, the voxels that demonstrated a higher activity in the Path and Manner conditions combined than the Identity condition were identified as functional ROIs (i.e., the voxels that are sensitive to moving stimuli). This subtraction was conducted simply to limit the voxels within which the contrast of interest (path vs. manner) would be probed. The contrast between the Path and the Manner condition was measured in a random-effect analysis by the *t*-value of the averaged time series of each voxel in individual functional ROIs. Finally, the distribution of these *t*-values from each ROI across participants were compared against zero to determine whether the motion-sensitive voxels in different anatomical ROIs showed preferential activation to the path or manner attribute of a moving event.

1.2. Results

1.2.1. Behavioral data

The accuracy and reaction time of the participants' manual responses in each condition were recorded and summarized in Table 1. The one-back task in the three conditions was performed accurately with a mean error rate lower than 10%, despite a marginally lower accuracy rate in the Path than the Manner condition ($t = 2.28$, $p = .06$) and than the Identity condition ($t = 1.89$, $p = .09$). Such findings suggest that the Path condition was slightly more difficult than the other two conditions, which might be caused by the similarity between the 18 paths that the starfish can possibly perform within the restricted area. The statistical analysis on the reaction time revealed differences among all three conditions (all $ps < .01$). The response based on the path attribute took longer than the response based on the manner attribute ($t = 3.32$, $p = .01$). However, the longer reaction time might be partly due to the characteristic of the task. Specifically, the path of a moving event can only be fully determined at the end of a movie, while the manner can be perceived after few frames, and the color/pattern can be perceived instantly.

1.2.2. Imaging data

Table 2 shows the mean size of the functional ROI of motion within each anatomical ROI (i.e., the number of voxels showing higher activation in the Path and Manner conditions combined than the Identity condition). A *t*-test contrasting the MR signal in the Path and the Manner condition (i.e., the difference in the Path and Manner conditions) was performed on every voxel within the functional ROI. The averaged *t*-value of this contrast within each ROI is also listed in Table 2. The motion-sensitive voxels within bilateral inferior occipito-temporal cortexes showed greater activation in the Manner than the Path condition (left: $t_7 = -3.61$, $p = .0086$; right: $t_7 = -5.32$, $p = .0011$). In contrast, the functional ROIs in dorsal regions, namely, bilateral IPLs and SPLs, demonstrated the opposite bias (left IPL: $t_7 = 5.94$, $p = .0006$; right IPL: $t_7 = 5.54$, $p = .0009$; left SPL: $t_7 = 4.21$, $p = .0040$; right SPL: $t_7 = 4.58$, $p = .0026$) (also see Fig. 1).

Very few voxels in the parahippocampus and the fusiform gyrus demonstrated motion sensitivity (see Table 2). The left parahippocampus showed greater activity for path over manner processing ($t_7 = 2.81$, $p = .0260$), while the right fusiform gyrus showed the opposite ($t_7 = -2.47$, $p = .0428$). We interpret these findings with caution, since these contrasts were mainly derived from few voxels. Path may have activated scene representations in the parahippocampus more than the manner attribute, whereas manner emphasized the face-like properties (which had eyes) and/or the human-body-like form of the starfish figures and activated the face/body representation in the posterior fusiform gyrus more than the path attribute.

Although the reaction times were longer in the Path than the Manner condition, we do not think that this difference is solely caused by the task difficulty between these two conditions. Even though the one-back task based on the path attribute was harder than that based on the manner attribute, the present fMRI results cannot be fully accounted for by the difficulty explanation, given that bilateral inferior occipito-temporal cortexes were more responsive to the alleged easier (i.e., Manner) condition. To directly control for the possible influence of task difficulty, which might be reflected in reaction times, we compared the contrast between the Path and Manner condition (i.e., the *t*-values) in the

Table 2
The size of the functional ROIs (i.e., the number of voxels that showed a motion main effect), and the direct contrast in each ROI (i.e., the *t*-value contrasting the MR signal of the Path and Manner conditions averaging across the voxels in the functional ROI) of Experiment 1

	PPA	FFA	Inferior occipito-temporal cortex	Middle/superior temporal cortex	IPL	SPL
Left hemisphere						
Number of voxels in the functional ROI (i.e., showing the motion main effect)	1 ± 1	7 ± 6	39 ± 19	35 ± 21	23 ± 16	33 ± 20
Contrast of Path–Manner (averaged *t*-value of difference)	1.43 ± 1.44	0.32 ± 1.38	−3.73 ± 2.92	0.98 ± 1.56	3.96 ± 1.89	5.06 ± 3.40
t	2.81	−0.66	−3.61	1.78	5.94	4.21
p	0.0260*	0.5317	0.0086*	0.1189	0.0006*	0.0040*
Right hemisphere						
Number of voxels in the functional ROI (i.e., showing the motion main effect)	1 ± 1	10 ± 5	61 ± 40	44 ± 20	26 ± 18	36 ± 33
Contrast of Path–Manner (averaged *t*-value of difference)	0.53 ± 0.83	−1.75 ± 2.01	−3.92 ± 2.08	0.51 ± 2.86	3.27 ± 1.67	4.94 ± 3.06
t	1.82	−2.47	−5.32	0.50	5.54	4.58
p	0.1118	0.0428*	0.0011*	0.6302	0.0009*	0.0026*

A *t*-test was further performed on the contrast between the Path and Manner conditions against zero.

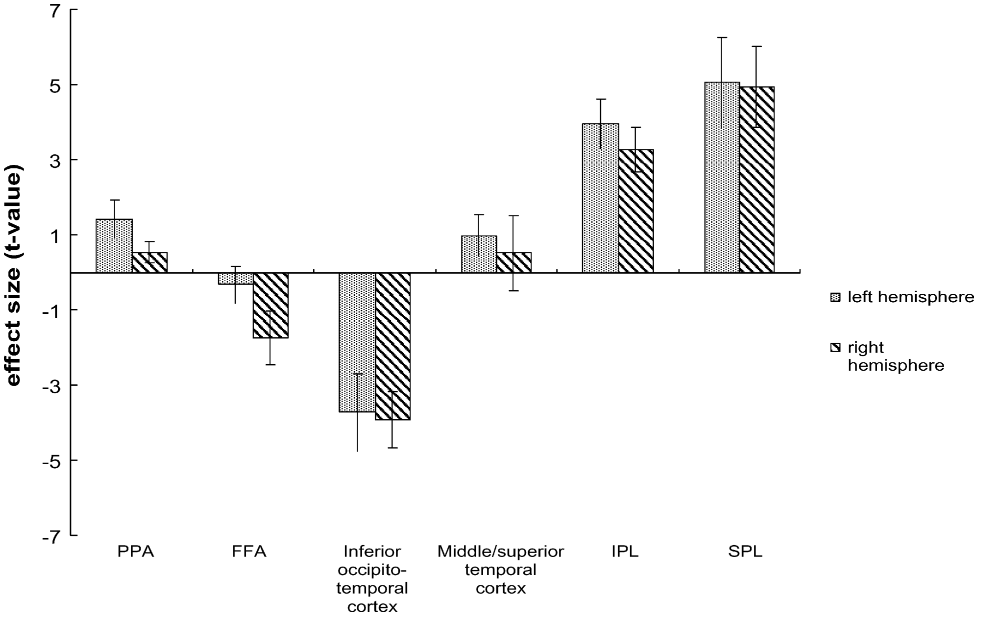

Fig. 1. In Experiment 1, direct contrast between path and manner processing within those voxels showing a motion main effect associated performing the one-back task according to path information with bilateral SPLs, bilateral IPLs, and left para-hippocampus. In contrast, performing the one-back task according to manner information was associated with bilateral inferolateral occipital-temporal regions and right fusiform gyrus.

functional ROIs within each anatomical ROI while treating the RT difference between the Path and Manner condition as a covariate. After taking out the contribution from the reaction time difference between the two critical conditions, the motion-sensitive voxels in bilateral SPLs and IPLs still showed higher activation in the Path than the Manner condition (all ps < .006), whereas such voxels in bilateral inferior occipito-temporal cortexes showed the opposite activation pattern (both ps < .015).

Overall, the data from Experiment 1 support our predictions. Within different regions sensitive to motion, dorsal regions were preferentially activated by the path condition and ventral regions were preferentially activated by the manner condition. We interpret such segregated neural processing of path and manner information as evidence for distinct perceptual components of motion representation, which are in parallel with the separate linguistic constituents to describe a moving event. We are agnostic about whether the neural substrates underlying the perceptual processing of path and manner information directly support the linguistic processing of path and manner information. We did not give participants instructions to prevent them from using verbal strategies to perform the one-back task. However, the brain regions that were associated with manner processing in the current experiment (i.e., bilateral inferior occipito-temporal cortexes) were close to but did not overlap with the left posterior middle temporal gyrus (MTG) and posterior STS (pSTS), areas associated with verb processing in our previous studies (Kable et al., 2002, 2005).

Experiment 2 was designed to extend Experiment 1. In Experiment 1, the starfish in the Path condition moved along a path without any manner movement, while the starfish in the Manner condition only moved with a manner without any path movement. Therefore, the stimuli in these two conditions differed in the area that they covered and possibly the eye movements that they induced. To control for these potential confounds, we used identical stimuli in both conditions in Experiment 2. Participants' attention was directed to either the path or the manner of the moving starfish. If the distinction between the two components of an action still occurred, then we would infer that the segregation of these motion attributes is rendered not just because of differences in the attributes of the stimuli, but also by top-down attentional selection of these attributes.

2. Experiment 2

We employed identical movies of moving events while directing the participants' attention to either the path or the manner of the stimuli. In addition to analyzing the imaging data via the ROI approach employed in Experiment1, we also performed a whole brain group analysis in this experiment.

2.1. Methods

2.1.1. Participants

Fourteen volunteers (ten men and four women) from the same pool and met the same criteria as in Experiment 1 were recruited in this experiment. None of them participated in this study before.

2.1.2. Materials and design

Similar to Experiment 1, every participant received three scans, each of which consisted of six blocks of each of the Path, Manner, and Identity conditions. Within each scan, the three conditions were presented in a pseudo-randomized fashion every three blocks. The stimuli of the Identity condition were identical to those that were employed in Experiment 1. As for the stimuli in the Path and the Manner condition, 18 new movies featuring the same purple starfish were prepared. Each movie lasted 3 s with 30 frames per second. In each of these new movies, the animated starfish moved along one out of six possible paths while performing one out of six possible manners, but none of these 18 movies had the same combination of a path and a manner. Critically, these 18 movies were employed in both the Path and Manner conditions, with different presentation orders. That is, the stimuli were identical in the Path and the Manner condition while only the participant's attention to different attributes of a moving event was manipulated in the one-back task.

Similar to Experiment 1, the stimuli in every condition were presented twice in every scan, which resulted in 30 trials with equivalent "same" and "different" trials in the one-back task. The same set of materials was repeated in the three scans with different orders of presentation. Special care was taken in arranging the presentation orders of the movies, so that the correct performance in the Path and Manner conditions could only be reached when the participants' responses were based on the intended motion attribute but not the other irrelevant one.

2.1.3. Procedures

All the procedures (including the imaging procedures) were identical to those of Experiment 1.

2.1.4. fMRI data analyses

The pre-processing of individual participants' imaging data was identical to that in Experiment 1. In addition to the ROI analysis conducted in Experiment 1, a whole brain group analysis was also performed. For each participant, the whole-brain data after pre-processing were normalized onto a standard coordi-

Table 3
The accuracy (%) and reaction time (in ms) in the three conditions of the one-back task from Experiment 2

	Path	Manner	Identity
Accuracy (%)	74.4	83.7	97.3
Reaction time (ms)	1528.33	1380	725

nate space (MNI) using a 12-parameter affine transformation with non-linear deformations. Normalization parameters were initially calculated using each participant's high-resolution anatomical scan. The same voxel-wise analysis via a general linear model as in the ROI analysis was performed on the normalized data from individual participants. The results were then spatially smoothed with a kernel with full-width half-maximum (FWHM) of three voxels. A random-effect analysis of the contrasts of interest (i.e., the motion main effect, the contrast between the Path and the Manner condition) was conducted to examine whether the mean value across participants in each voxel was significantly different from zero. For each contrast of interest, permutation methods (Nichols & Holmes, 2002) were used to determine the exact threshold for the desired map-wise false positive rate (i.e., $p < .05$).

2.2. Results

2.2.1. Behavioral data

The patterns of the accuracy and reaction time data from Experiment 2 were similar to that of Experiment 1 (see Table 3). The Path condition had the highest error rate, followed by the Manner condition, then the Identity condition. Most importantly, however, there was no difference between the Path and the Manner conditions ($t = 2.06$, $p = .11$). Attending to the path of a moving object was not more difficult than attending to its manner when both attributes were present. The comparable accuracy of these two conditions in this experiment (in contrast to Experiment 1) might be due to a relatively easier Path task, given that there were only six rather than 18 possible paths. The reaction time difference between every two conditions was significant (all $ps < .03$), confirming the longest reaction time of the Path condition, followed by that of the Manner condition, and then that of the Identity condition. As mentioned earlier, longer reaction times in the Path than the Manner condition might be caused by the nature of the task but not necessarily reflect the task difficulty. Nonetheless, we treated the RT difference as a covariate in the contrast between the Path and the Manner condition in the analyses of the fMRI data to control for first order effects of this potential confound.

2.2.2. ROI analyses of the imaging data

The data from Experiment 2 replicated the major findings of Experiment 1 (see Table 4). Selective attention to either the path or the manner attribute was associated with segregated activation patterns despite the fact that the stimuli in the two conditions were identical. When performing the one-back task for path, bilateral IPLs and SPLs showed greater activations than when performing the same task for manner (left IPL: $t_{13} = 9.26$, $p < .0001$; right IPL: $t_{13} = 2.68$, $p = .0317$; left SPL: $t_{13} = 6.13$, $p = .0005$; right SPL: $t_{13} = 2.92$, $p = .0223$) (also see Fig. 2). Even after the RT difference in the two conditions was taken into account, this pattern remained albeit less significant for the regions in the right hemisphere (left IPL: $p < .001$; right IPL: $p = .071$; left SPL: $p = .003$; right SPL: $p = .055$). The inferior occipito-temporal cortex in both hemispheres demonstrated the opposite activation pattern (left: $t_{13} = -5.15$, $p = .0013$; right: $t_{13} = -7.65$, $p = .0001$), even after the first order effects of RT differences between the Path and the Manner condition were taken into account (both $ps < .001$).

Consistent with the findings in Experiment 1, relatively few voxels showed motion sensitivity within ventral occipital regions. Moreover, when contrasting the activation between path and manner processing, only the functional ROI in the right fusiform gyrus demonstrated greater activation for manner than path processing ($t_{13} = -4.75$, $p = .0021$). Given the well-documented role of the fusiform gyrus in face and body processing (e.g., Grill-Spector, Knouf, & Kanwisher, 2004; Kanwisher et al., 1997; Liu, Harris, & Kanwisher, 2002; Peelen & Downing, 2005; Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000), directing one's attention to the manner that was performed by an animated figure with a face might have increased the saliency of face-like features. We did not find differences between path and manner processing in either parahippocampal gyrus ($ps > .1449$).

2.2.3. The whole brain group analysis

According to a one-tailed permutation analysis, the contrast of a voxel with significantly higher activity in the motion (i.e., Path and Manner) conditions than the stationary (i.e., Identity) condition has to surpass the threshold of 7.088 when the whole-brain false-positive error rate is controlled at $p = .05$. It should be noted that the purpose of this analysis was simply to serve as an initial filter to identify the voxels within which the contrast of interest, path versus manner, would be examined. The functional neural network sensitive to motion (see Table 5 and the purple regions in Fig. 3) included the following regions in both hemispheres: the SPL and IPL (BA7 and 40), the posterio-lateral inferior/middle temporal gyri (BA37), the occipital cortex (BA17/18/19), the inferior and middle frontal gyri (BA44 and 6), anterior insula (BA47/48), the medial frontal cortex (BA8/32), and the cerebellum.

Table 4
The size of the functional ROIs (i.e., the number of voxels that showed a motion main effect), and the direct contrast in each ROI (i.e., the *t*-value contrasting the MR signal of the Path and Manner conditions averaging across the voxels in the functional ROI) of Experiment 2

	PPA	FFA	Inferior occipito-temporal cortex	Middle/superior temporal cortex	IPL	SPL
Left hemisphere						
Number of voxels in the functional ROI (i.e., showing the motion main effect)	3 ± 4	8 ± 8	73 ± 46	41 ± 23	46 ± 29	57 ± 31
Contrast of Path–Manner (averaged *t*-value of difference)	0.26 ± 0.94	0.05 ± 1.38	−3.53 ± 3.37	0.53 ± 1.76	1.89 ± 1.29	2.75 ± 1.96
T	1.64	0.90	−5.15	2.04	9.26	6.13
P	0.1449	0.4002	0.0013*	0.0802	<0.0001*	0.0005*
Right hemisphere						
Number of voxels in the functional ROI (i.e., showing the motion main effect)	3 ± 3	15 ± 15	82 ± 40	72 ± 38	58 ± 47	83 ± 46
Contrast of Path–Manner (averaged *t*-value of difference)	0.71 ± 1.71	−1.11 ± 1.43	−2.86 ± 2.46	0.19 ± 2.04	0.97 ± 2.33	1.64 ± 2.51
T	0.89	−4.75	−7.65	0.61	2.68	2.92
p	0.4042	0.0021*	0.0001*	0.5623	0.0317*	0.0223*

A *t*-test was further performed on the contrast between the Path and Manner conditions against zero.

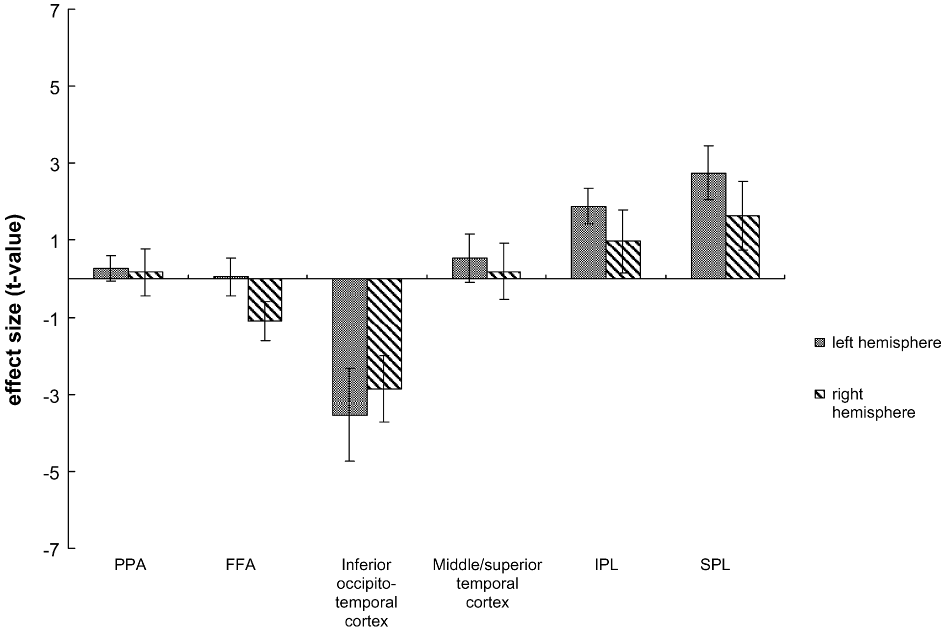

Fig. 2. In Experiment 2, bilateral SPLs and bilateral IPLs demonstrated higher activation when attending to path than manner information in performing the one-back task. In contrast, bilateral inferolateral occipital-temporal areas and right fusiform gyrus demonstrated the reverse pattern.

Within the functional network for motion perception, the permutation analysis indicated that the threshold of the 2-tailed contrast between the Path and the Manner condition is 6.04 to achieve a map-wise false-positive error rate at the .05 level. The results from this analysis converged with those of the ROI analysis. Within the regions showing a motion main effect (i.e., the purple areas in Fig. 3), attending to the path of motion was associated with the right SPL (BA7), left IPL (BA40), and bilateral posterior middle frontal gyrus (BA6), as the red areas shown in Fig. 3. In contrast, attending to the manner of the same action event was associated with bilateral posterior inferior/middle temporal cortex (BA37), as the green areas shown in Fig. 3. The direct comparison between the Path and the Manner condition revealed segregated neural substrates subserving selective attention to path and manner of motion, and supported our hypothesis that path and manner processing is associated with the dorsal and ventral part of the motion network, respectively.

3. Experiment 3

Both the ROI and whole-brain analyses in Experiment 2 demonstrated separate brain regions that were preferentially activated by selective attention to the path and the manner of motion. However, it is possible that the two conditions engaged the participant's eye movements differently. That is, although the participants were encouraged to watch the identical stimuli in the Path and Manner conditions from the beginning to the end of each movie, they might have followed the moving starfish longer with greater accompanying eye-movements in the Path than in the Manner condition. The association between path processing and the posterior parietal lobules and the frontal eye-field seems to be compatible with this speculation, since these regions are implicated in preparing and executing eye movements (Pierrot-Deseilligny, Milea, & Muri, 2004; Rafal, 2006). To determine if there were systematic dif-

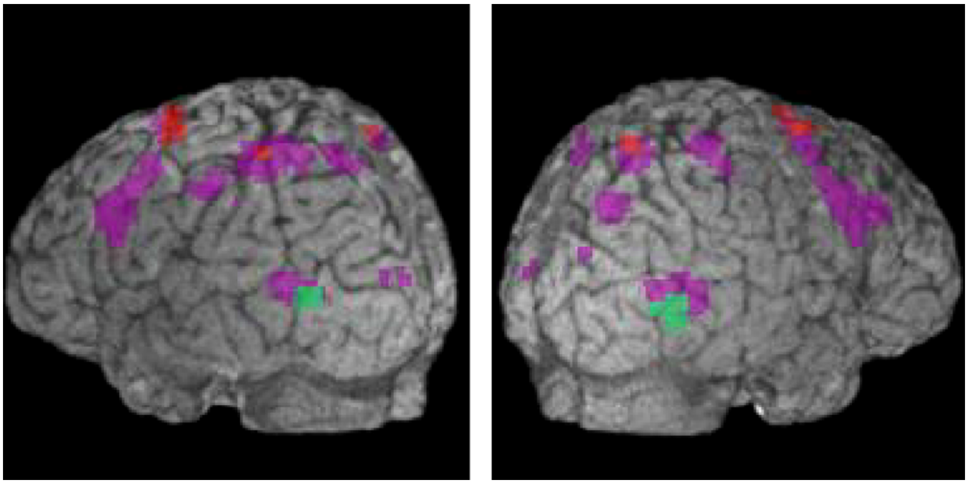

Fig. 3. The brain regions that demonstrated higher activity in the moving (path and manner) than stationary condition, including bilateral superior and inferior parietal lobules (BA7 and 40), posterior inferior/middle temporal gyri (BA37), occipital cortex (BA17/18/19), inferior and middle frontal gyri (BA44 and 6), anterior insula (BA47/48), medial frontal cortex (BA8/32), and cerebellum, were shown in purple ($t \geq 7.088$, $p < .05$, 1-tailed, as determined by permutation analyses). Among these regions, attending to path and manner was associated with the areas shown in red (right superior parietal lobule (BA7), left inferior parietal lobule (BA40), and bilateral frontal eye field (BA6), $t \geq 6.04$, $p < .05$, 2-tailed). In contrast, attending to manner was associated with bilateral posterior inferior/middle temporal cortex (BA37), as shown in green ($t \geq 6.04$, $p < .05$, 2-tailed).

Table 5
The coordinates of the regions that were associated with the motion main effect, selective attention to path information, and selective attention to manner information from the group data of Experiment 2

Regions with activation surpassing the threshold	BA	Tal coordinate
Motion main effect ($t \geq 7.088$, 1-tailed)		
Superior parietal lobule	L7	(18, −64, 52)
	R7	(−18, −64, 52)
Inferior parietal lobule	L40	(41, −33, 42)
	R40	(−41, −33, 42)
Posterior inferior temporal gyrus	R37	(−41, −51, −10)
Posterior middle temporal gyrus	L37	(47, −61, 4)
	R37	(−47, −61, 4)
Occipital cortex	L17	(12, −91, 8)
	18	(0, −74, 4)
	R19	(−26, −73, 35)
Inferior frontal gyrus	L44	(52, 11, 27)
	R44	(−52, 11, 27)
Middle frontal gyrus	L6	(25, 0, 55)
	R6	(−25, 0, 55)
Anterior insula	L47/48	(35, 21, −1)
	R47/48	(−35, 21, −1)
Medial fronal cortex	8	(0, 24, 45)
	32	(0, 23, 39)
Cerebellum		(+/−10, −71, −21)
Path preference ($t \geq 6.04$, 2-tailed)		
Superior parietal lobule	R7	(−14, −59, 55)
Inferior parietal lobule	L40	(37, −44, 55)
Middle frontal gyrus	L6	(25, 0, 55)
	R6	(−25, 0, 55)
Manner preference ($t \geq 6.04$, 2-tailed)		
Posterior inferior temporal gyrus	R37	(−48, −66, −1)
Posterior middle temporal gyrus	L37	(47, −69, 4)
	R37	(−49, −61, 4)

ferences in eye-movements across conditions, we conducted an eye tracking experiment.

3.1. *Materials and methods*

3.1.1. *Participants*

Eight volunteers from the community of National Central University in Taiwan who had not participated in this study before were tested in six blocks of each of the Path and Manner conditions.

3.1.2. *Materials, design, and procedures*

The procedures closely resembled those in Experiment 2, except that the Identity condition was not included, and the simultaneous fMRI data were not acquired. The participants performed the one-back task on the 18 movies of a moving starfish in a specific manner along a specific path while their attention was directed to either the path or the manner of the motion. That is, they made manual responses to indicate whether the path and the manner of the starfish in the current movie was the same as that in the previous movie in the Path and the Manner condition, respectively. The participants' eye-movements were simultaneously monitored and recorded every 2 ms throughout the experiment by an eye-tracker (EyeLink II, SR Research Ltd., Mississauga, Ontario, Canada).

3.1.3. *Results*

We found that that the eye-movements induced in the Path and Manner conditions did not differ. Specifically, the total average distance of the eye-movements of each movie was 50.69 and 52.69 degrees of visual angles in the Path and the Manner condition, respectively, and the difference between them was not significant ($t_7 = -1.22$, $p > .23$). To rule out the possibility that the participants might not have continued to track the starfish throughout the entire trial for the Manner as opposed to the Path condition, we also computed the distance between the first and the last gaze of each movie in different conditions. No difference was detected in this comparison, either (Path: 3.69 degrees of visual angles; Manner: 3.47 degrees of visual angles; $t_7 = 0.50$, $p > .63$). These data indicated that the eye-movements engaged in the Path and Manner conditions were similar, hence unlikely to account for the observed segregation of neural responsiveness to path and manner processing.

4. General discussion

In this study, we tested the hypothesis that the nervous system segregates motion in a way that parallels the linguistic parsing of a spatial event. Specifically, we examined whether path and manner of motion, two linguistically salient attributes of an event, are processed within different neural networks. Furthermore, we expected that the processing of these motion attributes to segregate along a dorsal–ventral axis, with path of motion being processed more dorsally than manner of motion.

Our findings provide strong support for this hypothesis. In both Experiment 1 and 2, the contrast between path and manner processing revealed distinct neural substrates that were preferentially involved in processing paths and manners of motion. The results of Experiment 2 replicated the findings of Experiment 1, and demonstrated that such segregation occurs under more stringent conditions. Specifically, when identical stimuli were employed in both the Path and Manner conditions, the participants' attention to path or manner of motion were associated with dorsal and ventral brain regions, respectively. Neural substrates in bilateral parietal lobules and frontal areas likely to include the frontal eye-field were responsive to path, while those in the bilateral posterior inferior/middle temporal cortex were responsive to manner of motion.

One account for the greater dorsal activations associated with processing the path than manner information of motion could be that attending to path was accompanied by greater eye-movements. On such an account, the control of eye movements, instead of the processing of path per se, could be producing differential activations. This account is unlikely to account for the results of the second experiment in which identical stimuli were used and in which no differences in eye movements were found when subjects performed this task off-line (as in Experiment 3). An intriguing possibility is that path information is encoded abstractly in eye-gaze coordinates that are neurally represented within networks involved in the control of eye movements.

The general idea that path and manner of motion are linked to conceptual and linguistic representations is supported by developmental and a few cognitive neuroscience studies. Infants are sensitive to path and manner information at different stages of development. In a modified preferential looking paradigm, Pruden et al. (2004) found that 10-month-old infants could extract an invariant path across different dynamic scenes, but the extraction of a common manner was not observed until 13-

month old. More interestingly, this sensitivity to path and manner of a moving event can be modulated by the degree of children's linguistic competence. Pulverman, Sootsman, Golinkoff, and Hirsh-Paset (2003) demonstrated that 14- to 17-month-olds with rich English vocabularies were more attentive to manner changes than to path ones. Within cognitive neuroscience, action recognition is associated with activations in a network distributed in lateral occipitotemporal, inferior parietal, and inferior prefrontal areas, including MT/MST and the regions in and near the superior temporal sulcus (STS)(Allison et al., 2000; Decety & Grezes, 1999; Kable & Chatterjee, 2006; Rizzolatti, Fogassi, & Gallese, 2001).[1]

Given that manner of motion is communicated most often by verbs while path is communicated most often by prepositions in English, one might expect a similar anatomic segregation for processing these linguistic constituents in English speakers/readers as we observed for the processing of the motion components. We have reported that processing verbs activates the left posterior middle temporal gyrus (MTG) and posterior STS (pSTS) (Kable et al., 2002, 2005), and others have found that naming prepositions activates the posterior inferior parietal lobule (Damasio et al., 2001; Emmorey et al., 2002). This general pattern is also corroborated by lesion studies (Tranel & Kemmerer, 2004; Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003). Recently we reported a similar ventral–dorsal split in lesions of the patients with comprehension deficits of thematic roles (determined by verbs) and locative relations (determined by prepositions) (Wu, Waller, & Chatterjee, 2007). These observations raise the possibility that the processing of path and manner of motion serves as perceptual points of entry for the neural mediation of prepositions communicating trajectories and verbs communicating actions. It also follows naturally that the neural substrates supporting path processing is the perceptual point of entry for verbs that express path information. Because there are only a handful of path verbs in English (e.g., enter, exit), this hypothesis could be tested in verb-framed languages (e.g., Spanish, Greek).

In addition to suggesting a parallel neural organization of perception and language, the results from the current study indicate that the perception of and attention to the path and manner information of a moving event also respects the dorsal–ventral split of "where-what" processing in the visual system. Another prominent theory, however, ascribes the dorsal and ventral streams as related to action ("how") and perception ("what"), respectively (Goodale & Milner, 1992). Path processing focuses on the changing location of objects in space, which is crucial to acting on or towards them (Goodale & Westwood, 2004). Thus, our finding of higher activation in the Path than the Manner condition is also consistent with this view.

In summary, we report evidence that the neural decomposition of higher-level motion processing follows the linguistic parsing of motion into different language constituents. These findings reinforce the notion that the neural substrates of language and space are linked and follow parallel principles of organization.

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[1] A prominent view of action comprehension is the mirror neuron theory. On this account people understand actions by enacting the actions within their own motor systems (Rizzolatti et al., 2001). We have not found strong support for this theory in our previous studies, and the activation of mirror neurons may be limited to the motor repertoire of the observer (Buccino et al., 2004). Another possibility is that actions are often composed of both manners and paths of motion, and the fronto-parietal activations observed in some action comprehension studies in part represent the processing of path information, while the posterior temporal activations represent the processing of manner information.

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