

See discussions, stats, and author profiles for this publication at: <http://www.researchgate.net/publication/229152359>

Dorsal stream activity and connectivity associated with action priming of ambiguous apparent motion

ARTICLE *in* NEUROIMAGE · JULY 2012

Impact Factor: 6.36 · DOI: 10.1016/j.neuroimage.2012.07.010 · Source: PubMed

CITATIONS

2

7 AUTHORS, INCLUDING:



[Kelly J Jantzen](#)

Western Washington University

44 PUBLICATIONS 1,142 CITATIONS

[SEE PROFILE](#)



[Matthew Seifert](#)

Florida Atlantic University

3 PUBLICATIONS 7 CITATIONS

[SEE PROFILE](#)



[Lawrence Behmer](#)

City University of New York - Brooklyn College

6 PUBLICATIONS 17 CITATIONS

[SEE PROFILE](#)

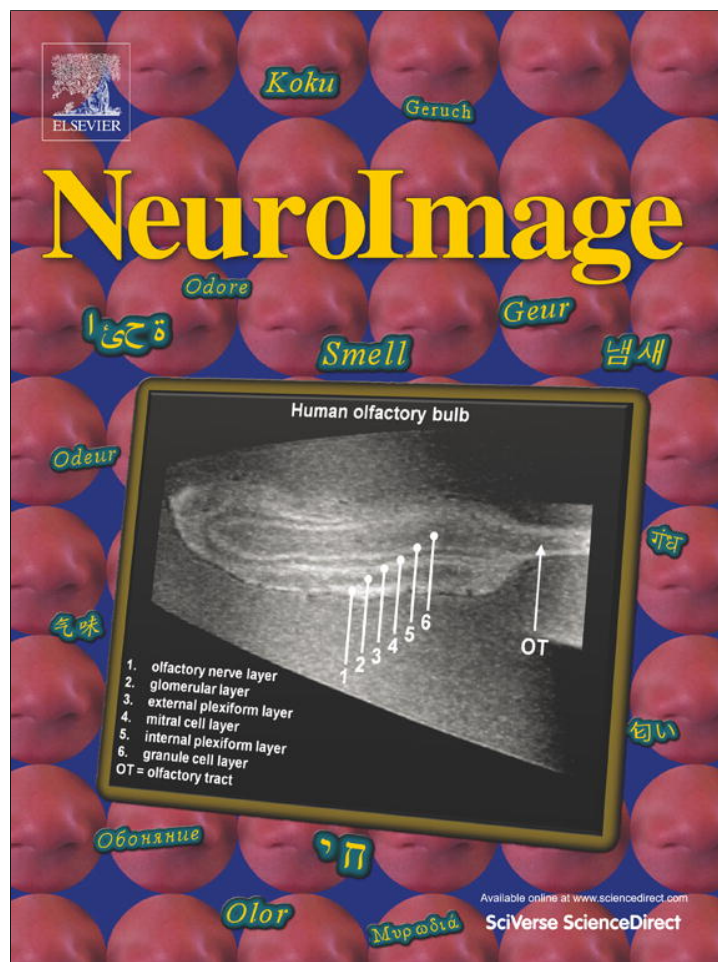


[Lawrence A Symons](#)

Western Washington University

30 PUBLICATIONS 677 CITATIONS

[SEE PROFILE](#)



(This is a sample cover image for this issue. The actual cover is not yet available at this time.)

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

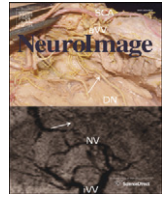
<http://www.elsevier.com/copyright>



Contents lists available at [SciVerse ScienceDirect](#)

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg



Dorsal stream activity and connectivity associated with action priming of ambiguous apparent motion

K.J. Jantzen^{*}, Matthew Seifert, Benjamin Richardson, Lawrence P. Behmer, Charles Odell, Aaron Tripp, Lawrence A. Symons

Western Washington University, USA

ARTICLE INFO

Article history:

Accepted 8 July 2012

Available online 14 July 2012

Keywords:

Sensorimotor integration

Common coding

Ambiguous apparent motion

Event-related desynchronization

Independent components analysis

Phase locking

ABSTRACT

Theories proposing a bidirectional influence between action and perception are well supported by behavioral findings. In contrast to the growing literature investigating the brain mechanisms by which perception influences action, there is a relative dearth of neural evidence documenting how action may influence perception. Here we show that action priming of apparent motion perception is associated with increased functional connectivity between dorsal cortical regions connecting vision with action. Participants manually rotated a joystick in a clockwise or counter-clockwise direction while viewing ambiguous apparent rotational motion. Actions influenced perception when the perceived direction of the ambiguous display was the same as manual rotation. For comparison, participants also rotated the joystick while viewing non-ambiguous apparent motion and in the absence of apparent motion. In a final control condition, participants viewed ambiguous apparent motion without manual rotation. Actions influence on perception was accompanied by a significant increase in alpha and beta band event related desynchronization (ERD) in contralateral primary motor cortex, superior parietal lobe and middle occipital gyrus. Increased ERD across these areas was accompanied by an increase in gamma band phase locking between primary motor, parietal, striate and extrastriate regions. Similar patterns were not observed when action was compatible with perception, but did not influence it. These data demonstrate that action influences perception by strengthening the interaction across a broad sensorimotor network for the putative purpose of integrating compatible action outcomes and sensory information into a single coherent percept.

© 2012 Elsevier Inc. All rights reserved.

Introduction

It is now widely accepted that perception can influence action planning and execution (e.g. [Blakemore and Frith, 2005](#); [Rueschemeyer et al., 2009](#)), in part by triggering motor related representations of perceptual stimuli ([Rizzolatti and Craighero, 2004](#); [Rizzolatti and Luppino, 2001](#)). Moreover, growing evidence clearly indicates that the influence of perception on action is mediated over the dorsal pathway ([Goodale and Milner, 1992](#); [Goodale and Westwood, 2004](#); [Rizzolatti and Matelli, 2003](#)) that includes the mirror neuron system ([Rizzolatti and Craighero, 2004](#)). Following the early insights of [James \(1890\)](#) and [Gibson \(1979\)](#) among others, there has been recent resurgence in the appreciation of the converse relationship; namely the ability of motor planning and execution to influence visual perception ([Hommel et al., 2001](#); [Prinz, 1997](#); [Schütz-Bosbach and Prinz, 2007](#)). In contrast to the wealth of literature investigating the neural mechanisms by which perception influences action, there is a relative dearth of evidence for the neural basis of the influence of action on perception.

Behavioral research consistently demonstrates the influence of action planning and execution on perception (see reviews in [Schütz-Bosbach and Prinz, 2007](#); [Zwicker and Prinz, 2012](#)). For example, action has been shown to influence the speed of visual processing ([Craighero et al., 1999](#); [Lindemann and Bekkering, 2009](#)), the judgment of another's actions ([Blaesi and Wilson, 2010](#); [Hamilton et al., 2004](#)) or facial expression ([Blaesi and Wilson, 2010](#)) and the perceived direction of ambiguous apparent motion ([Wohlschläger, 2000](#)). [Wohlschläger \(2000\)](#) asked participants to report the rotation direction of an ambiguous apparent motion display while manually turning a knob in either a clockwise or counterclockwise direction. Although the apparent motion display is equally likely to be perceived as rotating in a clockwise or anticlockwise direction, action primed the perception of the participants, who tended to judge the direction of the apparent motion stimulus to be the same as the direction of manual rotation. This finding of “perceptual resonance” has been interpreted as reflecting a bidirectional link between perception and action and considered as support for the existence of a shared neural representation of action and perception ([Schütz-Bosbach and Prinz, 2007](#); [Wohlschläger, 2000](#)). Nonetheless, data revealing the neural systems involved and how they function to support perceptual resonance is presently lacking. This study aims to investigate the large-scale neural dynamics

^{*} Corresponding author at: Western Washington University, Bellingham, Washington, 98225, USA. Fax: +1 360 650 7305.

E-mail address: Kelly.jantzen@wwu.edu (K.J. Jantzen).

underlying the ability of movement to prime or disambiguate perception.

Visual information critical for action planning and understanding is processed over dorsal cortical areas including visual, parietal, premotor and primary motor cortices (Goodale and Milner, 1992; Rizzolatti and Craighero, 2004; Rizzolatti and Luppino, 2001). Theories of common coding (Hommel et al., 2001; Prinz, 1997) and perceptual resonance (Schütz-Bosbach and Prinz, 2007) propose that action planning and perception share a common neural representation. Although the theories are somewhat ambiguous with respect to the underlying neural basis of the shared representations, Schütz-Bosbach and Prinz (2007) review evidence favoring the hypothesis that a bidirectional influence between perception and action is mediated by distributed brain circuits that include the well-studied dorsal visual stream and human mirror neuron system. The assumption is that the same neural pathways that mediate the influence of perception on action (e.g. Blakemore and Frith, 2005; Rizzolatti and Craighero, 2004), also allow for action to influence perception. Accordingly, perceptual resonance should be reflected across a distributed cortical network that may include extrastriate, parietal and motor cortices (Goodale and Milner, 1992). Transcranial magnetic stimulation (Cattaneo et al., 2010) and functional MRI studies support this hypothesis, demonstrating that goal directed action can modulate activity in the extrastriate body area (Astafiev et al., 2004) and that ongoing control of one's own actions influences visually mediated perceptual decisions via a brain network that includes motor cortex, inferior frontal gyrus, parietal cortex and extrastriate regions (Hamilton et al., 2004).

Synchrony of discrete neural populations in the gamma band provides a putative mechanism for action to influence perception. Substantial evidence supports the importance of neural synchrony in underlying effective integration across discrete subsets of neural populations (Varela et al., 2001; Womelsdorf and Fries, 2006). In particular, synchronization of oscillatory electrical brain activity in the gamma band (40 Hz) has been proposed as a basic neural mechanism for establishing the large-scale functional connectivity between distinct neural ensembles (Singer and Gray, 1995) proposed to underlie coherent perception and cognition (Bressler and Kelso, 2001; Varela et al., 2001). Experimental findings have largely supported such hypothesis, linking large-scale neural integration in the gamma band to cross modal binding (Senkowski et al., 2008), the formation of stable visual percepts (Doesburg et al., 2009), local feature binding (Rose and Büchel, 2005) selective attention (Doesburg et al., 2008) and sensory-motor integration (Womelsdorf and Fries, 2006). Thus common coding of visual and motor representations may involve increased gamma binding among distributed dorsal visuomotor processing regions.

Here we used EEG to investigate the hypothesis that perceptual resonance, that is the ability of action to influence perception, is mediated by neural activity over the dorsal stream connecting primary visual and motor cortices. We further propose that the influence of action on perception is dependent on large-scale neural integration across this circuit as reflected in gamma band synchrony between discrete neural ensembles. Following Wohlschläger (2000), participants manually rotated a joystick in a clockwise or counter-clockwise direction while viewing an ambiguous apparent motion stimulus. Bias or priming of perception by action is indicated when participants report rotation of the ambiguous display in the same direction as manual rotation. We predict that this form of "perceptual resonance" will be accompanied by an increase in localized activity, as indexed by event related desynchronization in the alpha and beta bands, and long-range gamma coupling across cortical visual-motor circuits. For comparison, participants also viewed non-ambiguous apparent motion during manual rotation of the joystick. This important control includes equivalent sensory and motor components because the joystick is rotated in the same direction as the apparent motion stimulus. The direction of visual motion, however, is not ambiguous and therefore manual rotation does not prime or disambiguate visual perception. Additional controls included manual

rotation in the absence of apparent motion and viewing an apparent motion display in the absence of manual rotation.

The primary motor cortex is well recognized for its role in movement production (Kakei et al., 1999). In the EEG, voluntary action is accompanied by a decrease in alpha and beta band power (Pfurtscheller and Lopes da Silva, 1999) localized to the contralateral primary somatosensory and motor strip (Cheyne et al., 2006). A similar pattern of alpha and beta event related desynchronization is also reported during the observation of action (Hari et al., 1998) and when viewing visual stimuli with acquired action relevance (Behmer and Jantzen, 2011) indicating that primary sensorimotor regions may play a broader role in action representation. Perception of visual apparent motion involves a number of dorsal stream areas including regions of the medial temporal lobe (MT/V5) (Corbetta, 1990; Goebel et al., 1998; Muckli et al., 2002) and parietal cortex (Sterzer et al., 2009; Williams et al., 2003). These extrastriate and parietal regions areas are also important for resolving conflict in ambiguous displays and in the top down modulation of visual perception (reviewed in Sterzer et al., 2009) and therefore should also demonstrate event related desynchronization when participants view ambiguous apparent motion. Moreover, in keeping with our prediction that common coding of action and perception is mediated by an increase in neural coupling, we predict an increase in gamma band synchrony between motor cortex and both parietal and extrastriate regions when motor action primes visual perception.

Materials and methods

Participants

Data were acquired from 19 participants (12 male) with a mean age of 23.9 ($SD = 6.1$) years. All participants were strongly right handed as determined using a revised version of the Edinburgh handedness inventory (Oldfield, 1971). All participants had normal or corrected vision and self reported being free from neurological disorders. Participants provided written informed consent and were treated in compliance with the IRB of Western Washington University.

Apparatus

Participant's movements were recorded using an analog joystick fixed to a small table and placed so that it was comfortably accessible to the participant's right hand. The X and Y-axis position of the joystick was digitized and recorded as two separate channels in the EEG record. Vision of the hand was occluded by a black screen placed along the participant's line of site to the joystick.

Stimuli were comprised of a circular array of 6 black dots 1 cm in diameter (Fig. 1). For ambiguous motion conditions two frames of the circular array were alternated every 400 ms. The location of the dots in the second frame was rotated 30° with respect to the first. This stimulus results in the perception of ambiguous apparent motion during which participants perceive rotation of the dots in either the clockwise or counter-clockwise direction. For the Directed motion condition non-ambiguous apparent motion was created using four frames presented in sequence every 200 ms. The shorter presentation interval was necessary to ensure the same perceived angular velocity across conditions. To create the perception of clockwise apparent motion each successive frame was rotated 15° in the clockwise direction (Fig. 1B). Similarly, we created counter-clockwise apparent motion by rotating each frame 15° in the counter-clockwise direction. Stimuli presentation was controlled by custom software created in Visual Basic 5.0 and run under Windows XP on a Dell Precision Workstation. Stimuli were viewed on a 19-inch LCD monitor viewed from a distance of approximately 60 cm. The circular array was 12 cm in diameter and subtended a visual angle of approximately 11.5°.

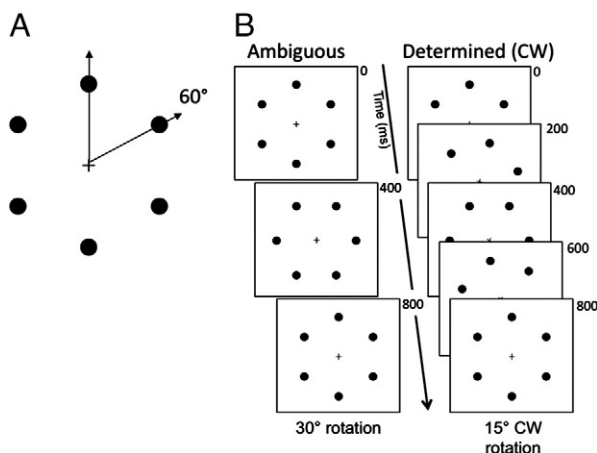


Fig. 1. The apparent motion stimulus was created from of an array of 6 solid dots arranged in a circle at 60-degree intervals around a central fixation point (A). Ambiguous apparent motion was created by alternating every 400 ms. between the dot array in A and a second array in which the dots were rotated 30°. Non-ambiguous apparent motion was created using 4 arrays presented in sequence every 200 ms. Each array was rotated by 15° (either clockwise or counter-clockwise) with respect to the preceding array in the sequence.

Procedure

A visual cue that instructed participants about how to move was presented at the onset of each 6.6-second trial. A single black dot presented to the right or left of a central fixation-cross instructed the participant to move in a clockwise or counter-clockwise direction respectively. Dots appearing simultaneously on both sides of fixation instructed the participant not to move. Participants were instructed to maintain a comfortable movement rate of approximately 1 revolution/second. A practice trial was used to establish an appropriate rotation speed. After 1-second participants were presented with apparent motion stimuli perceived as ambiguous with respect to the direction of rotation (Ambiguous) or non-ambiguously moving clockwise or counter-clockwise (Determined). The combination of movement and apparent motion stimuli resulted in 4 experimental conditions (56 trials per condition) presented in a randomized order. For the main experimental conditions, participants moved the joystick in either the clockwise or counter-clockwise direction while viewing ambiguous apparent motion (A) or determined apparent motion (D). Two additional control conditions were created by presenting the ambiguous apparent motion stimulus in the absence of movement (Stimulus only, S) and by having participants rotate the joystick in the clockwise or counter-clockwise direction in the absence of apparent motion (Movement only, M). For the M condition participants viewed a single static frame of the apparent motion stimulus. At the end of each trial, participants pressed a left or right response key to indicate that they perceived rotation of the apparent motion stimulus in the counter-clockwise or clockwise direction respectively. For M trials, button pressed indicated the direction of joystick rotation.

EEG recording

EEG was recorded from 64 Ag/AgCl active electrodes using a Biosemi (Amsterdam, Netherlands) Active Two system. Electrodes were mounted in an elastic head cap configured in a 10–10 configuration (Oostenveld and Praamstra, 2001). Signals were conducted using a saline-based conductive gel (Signa Gel) and all offsets were maintained below 20 μ V. Unreferenced signals were amplified and digitized to disk at 512 Hz using Biosemi amplifiers and acquisition software. After data collection we found that electrode FT8 malfunctioned for a majority of the participants. Therefore, we removed FT8 from further analysis. Raw EEG signals were referenced to the average of all channels and bandpass filtered

between 1 and 50 Hz. Single trial epochs extending from -1.0 s to 5.6 s around the onset of the apparent motion stimulus were extracted from the larger data record.

Behavioral analysis

Channels containing joystick position information were bandpass filtered between 1 and 5 Hz and normalized to the range -1 to 1 . Rotation direction and speed were determined from the angular velocity calculated as the first derivative of the polar angle of the X and Y position divided by the sample rate. The angular velocity was averaged across the trial to provide a representation of movement direction (positive or negative velocity) and rotation speed. Trials in which participants did not move in the instructed direction were excluded from analysis. Average rotation velocity was determined for each participant and condition by averaging the absolute value of the rotation velocity across trials for the A, D and M conditions. Taking the absolute value allowed for us to collapse across clockwise and counter-clockwise trials.

The average of the perceived direction of rotation was expressed in terms of the percentage of trials the participant reported clockwise rotation. Because we were interested in the neural basis of the influence of movement on perception, for the A and D condition, only trials in which participants reported motion in the same direction as their movement were retained for further EEG analysis.

EEG decomposition and analysis

Analysis was performed using the EEGLAB toolbox (Delorme and Makeig, 2004) and custom scripts running under Matlab 7.9. Source activity was identified and analyzed using an established independent component clustering approach (see Onton et al., 2005; Ward and Doesburg, 2009; Ward et al., 2010). The benefit of this approach is that it allows us to perform analysis on the unmixed signals in source space rather than in the linearly mixed signals characteristic of sensor space.

We then decomposed the concatenated trials from all conditions into 63 maximally independent EEG components (IC) using EEGLAB. IC sources were localized in EEGLAB by fitting a single equivalent current dipole to the scalp potential using a boundary element model. Only ICs with scalp maps for which the single dipole source was located within the brain and had less than 15% residual variance (RV) were included in the subsequent analyses. One participant's data was removed at this stage because excessive noise resulted in the selection of too few components. For the remaining 18 participants, this procedure results in the selection of an average of 12.3 components (± 4.4) with a range between 8 and 19 components.

To determine which neural sources were common to a group of subjects, a cluster analysis of all valid ICs was performed based on the dipole locations. A k-means clustering algorithm separated a total of 210 valid ICs into 18 clusters. If a cluster contained more than one IC from an individual participant, then only the IC with the lowest RV was retained in the cluster. The neural region represented by each dipole cluster was estimated by averaging the Talairach coordinates of the dipoles in the cluster.

A time/frequency decomposition was then performed on the time series of each IC. Wavelet coefficients were estimated at 95 equally spaced frequencies from 3 to 50 Hz and 200 time points from -1 to 5.6 s, using Gaussian tapered complex Morlet wavelets (see Delorme and Makeig, 2004). To balance the trade off between spectral and temporal resolution, we used a 3-cycle wavelet at the slowest frequency and increased the number of wavelets by a factor of 0.5 at each frequency bin. Event related spectral perturbations in power (ERSP) were computed in each frequency by normalizing the power spectral estimate in each frequency bin by the mean power level during the prestimulus baseline according to the equation $ERSP_{ft} = 10 \cdot \log_{10}(p_{ft}/p_{base})$, where p_{ft} is the mean wavelet estimate for frequency bin f and time point t averaged over

trials, and $phase_i$ is the wavelet estimate in frequency bin f averaged over trials and sample points from the pre-stimulus period. Decreases in spectral power from baseline indicate an increase in neural activity and are referred to as event related desynchronization (ERD) whereas increases in power indicate a decrease in neural activity and are referred to as event related synchronization (ERS) (Pfurtscheller and Lopes da Silva, 1999). Fig. 3 shows representative data from each stage of analysis. We also computed the Phase Locking Value (PLV; Lachaux et al., 1999) in each frequency band for all component pairs as a measure of neural integration between brain regions (Varela et al., 2001). The phase (Φ) between IC pairs i and j at each time point and frequency bin was computed according to the equation $\Phi_{ij} = 1/n \sum [p_{ik} \cdot p_{jk}^* / |p_{ik} \cdot p_{jk}^*|]$, where n is the number of single trials and $*$ indicates the complex conjugate. The resulting PLV adopts a value between 0 and 1 with a phase locking value near one indicating a consistent phase relationship over trials and a value near zero indicates an inconsistent or random phase across trials.

To characterize task dependent changes in local oscillation brain activity and phase locking we averaged the time frequency activity and the PLV over the time interval from 1000 to 5000 ms after the onset of the apparent motion stimulus separately for the alpha (8–12 Hz), low beta (12–20 Hz), high beta (20–30 Hz) and gamma (30–50 Hz) bands. The time range selected eliminated transient responses related to visual stimulus onset and provided a single estimate of the wavelet coefficient and phase locking for each IC (or IC pair), band, participant and condition. Differences in band power and phase locking between experimental conditions were assessed using repeated measures analysis of variance. Post-hoc t tests Bonferroni corrected for the number of cluster pairs ($\alpha = 0.005$) were used to evaluate differences between individual pairs of conditions.

We adopted a data driven approach to identifying IC clusters of interest. In order for an IC cluster to be considered for analysis, the oscillatory power in at least one frequency band had to differ between experimental conditions (1-way ANOVA). An increase in local task-related brain activity nominally results in decreased oscillatory power (ERD) within alpha and beta bands and may also result in an increase in oscillatory power in gamma band. Nonetheless, because the ANOVA found no significant effects in the gamma band, subsequent analysis defined neural activity in terms of ERD. Paired t -tests were used to further classify IC clusters into two categories. First we defined task related clusters as those demonstrating greater desynchronization (in at least one frequency band) for conditions in which apparent motion and action occurred together (A and D) compared to when action (M) or apparent motion (S) occurred in isolation. Note that this approach identifies clusters related exclusively to sensory or motor demands of the task as well as clusters related to visuomotor integration. Second, we defined priming related clusters as any cluster demonstrating greater desynchronization (in at least one frequency band) when action successfully primed vision (condition A) than when action and vision occurred together in the absence of priming (condition D). An alpha level of 0.005 was adopted to fortify against false positives owing to multiple comparison.

The evaluation of the PLV was restricted to the task related and priming related clusters. We were primarily interested in how coupling between motor and visual areas was modulated by the combination of movement and perception and, in particular, how movement in the presence of ambiguous motion differed from conditions in which movement did not influence perception. As such, we further restricted statistical evaluation of the PLV to the 3 conditions in which the motor system was engaged (A, D, M), and eliminated the S condition because no motor cortex activity was present during this condition. A one-way ANOVA identified IC pairs in which phase coupling varied significantly across conditions.

Results

Behavior

The average rotation speed across participant and condition was 1.27 ($SD = 0.51$) revolution/second. A repeated measures analysis of variance indicated that rotation speed did not differ across conditions, $F(2, 34) = 0.691$, $p = 0.508$. The mean and standard error for each condition is shown in Fig. 2A.

Inspection of the perceived direction of rotation confirmed that the experimental conditions successfully generated the expected perceptual effects. When viewing ambiguous apparent motion in the absence of action, participants reported clockwise rotation at a rate of 55.05% ($SD = 22.79\%$). A one sample t -test confirmed that this value was not significantly different from the expected mean of 50%, $t(17) = 1.02$, $p = 0.32$. For the D condition participants clearly perceived rotation to be in the determined direction. The percentage of trials on which rotation was perceived as clockwise was 99.32% ($SD = 1.83\%$) and 0.74% ($SD = 1.57\%$) for clockwise and counter-clockwise conditions respectively.

For the ambiguous direction condition (A) the direction of manual rotation strongly influenced the perceived direction of apparent motion. When rotating the joystick clockwise participants perceived clockwise motion on 73.86% ($SD = 17.16\%$) of trials. When rotating counter-clockwise, participants perceived clockwise motion on 25.96% ($SD = 20.84\%$) of trials. Perceived percentage of clockwise rotation was significantly different between these two conditions, $t(17) = 6.36$, $p < 0.001$ and both clockwise, $t(17) = 6.37$, $p < 0.001$ and counter-clockwise rotation, $t(17) = 5.28$, $p < 0.001$ differed significantly from the hypothetical mean of 50%. For A and D conditions, only trials on which participants perceived apparent motion in the same direction as manual rotation were included in EEG analysis. The mean and standard error of perceived clockwise rotation is shown in Fig. 2B.

EEG

Our classification approach resulted in the identification of 5 task related component clusters (see Table 1) located in left precentral

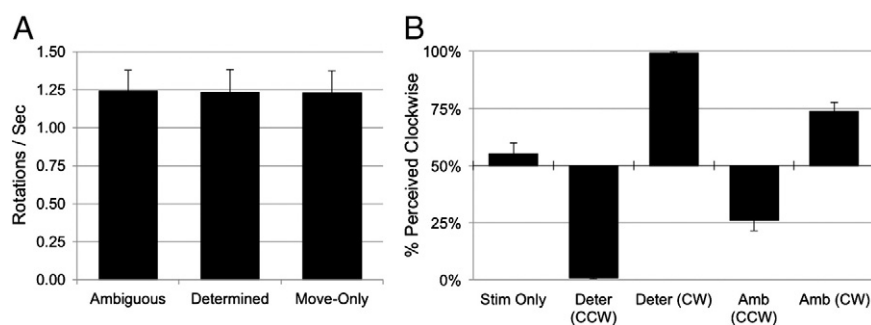


Fig. 2. (A) The mean rotation speed across participants for the manual rotation conditions (A: ambiguous; D: determined; M: movement only). The percent of trials on which participants perceived apparent motion moving in a clockwise direction is shown for each apparent motion condition. (S: Stimulus only; CW: clockwise; CCW: counter clockwise).

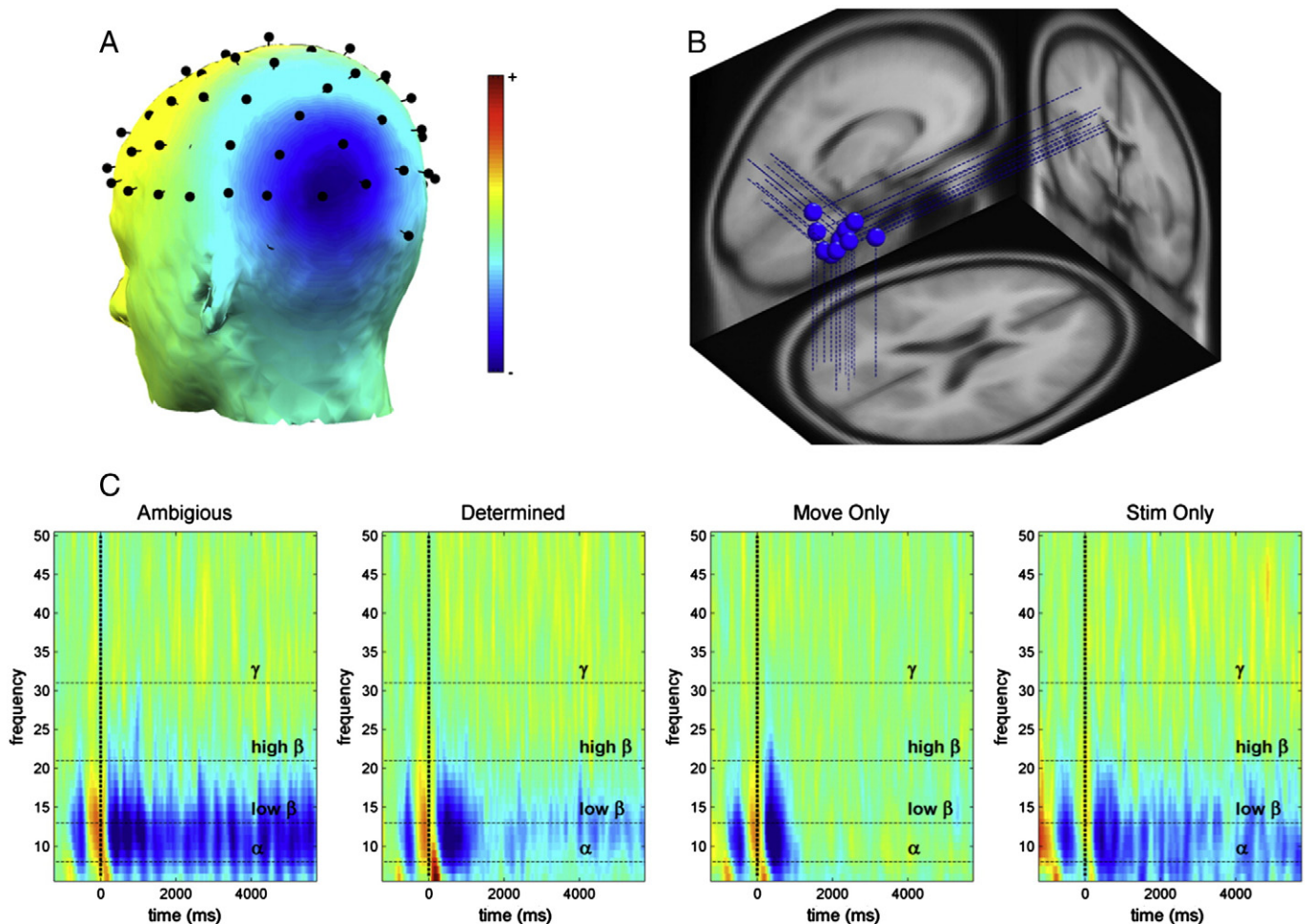


Fig. 3. Representative data illustrates key stages of EEG analysis. (A) A single independent component pattern is plotted on a three-dimensional model of a standardized head. Black spheres indicate EEG electrode locations. (B) A left parietal cluster of equivalent current dipoles (ECD: spheres) is projected onto axial, coronal and sagittal MRI slices. Each ECD is from a different participant and represents the computed location of the neural source of a single independent component. One of the dipoles corresponds to the pattern in (A). (C) Time-frequency plots computed from the time series of the independent components from the cluster in (B). The time domain data for each source was converted to a time/frequency representation before averaging separately for each condition. The log power for frequencies in the range from 3 to 50 Hz is shown in a time window from 1 s before to 6 s after the first onset of the visual stimulus array. Blue colors indicate a decrease in oscillatory power from the pre-stimulus period and red colors indicate an increase in oscillatory power. Standard frequency bands are shown for reference (α : alpha, 8–12 Hz; low β : low beta, 12–20 Hz; high β : high beta, 20–30 Hz; γ : gamma, 30–50 Hz). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

gyrus, left superior parietal lobe (SPL), left middle occipital gyrus (MOG), right occipital cortex (OCC) and posterior cingulate (Cing). The left precentral gyrus cluster was located in Brodmann area 4 on the side contralateral to the moving limb, an area compatible with the primary sensorimotor cortex (SMC). The specific oscillatory bands in which significant results were obtained are presented for each cluster in Table 2.

The posterior cingulate and occipital clusters were task related but not priming related. For both clusters, a localized increase in neural

activity is indicated by sustained alpha and beta band desynchronization (blue) throughout the post-stimulus period for the Ambiguous and Determined conditions (Fig. 4). In the posterior cingulate cluster, alpha and beta ERD was significantly greater during the A and D conditions than during the S condition (see Table 2 and Fig. 4). Within the occipital cluster, event related alpha and low beta desynchronization was significantly greater in the A and D conditions compared to the M condition (see

Table 1

The Cartesian and anatomical center of clusters demonstrating task related and priming related patterns of activity. IC: the number of participants in the cluster. RV: the mean residual variance of equivalent current dipoles in the cluster.

Cluster	Hem.	Anatomy	BA	X	Y	Z	IC	RV
<i>Task related clusters</i>								
OCC	R	Right occipital lobe	17	20	−91	9	6	5.20
Cing	L	Posterior cingulate	29	−2	−42	15	10	8.72
<i>Priming related clusters</i>								
SMC	L	Precentral gyrus	4	−35	−21	57	10	3.69
SPL	L	Superior parietal lobe	7	−13	−53	45	12	4.61
MOG	L	Middle occipital gyrus	19	−30	−74	23	11	4.63

Table 2

Frequency bands in which clusters met the statistical criteria for classification as task and priming related (indicated by an X). Specifics of significant contrasts are indicated by capital letters and described below the table.

Cluster	Task related			Priming related		
	α	$\beta 1$	B2	α	$\beta 1$	B2
Cing	X _B	X _B	X _C			
OCC	X _A	X _A				
M1	X _A	X _A	X _A	X	X	X
SPL			X _A			X
MOG	X _B	X _B		X	X	

A: A and D conditions > M.

B: A and D conditions > S.

C: A and D conditions > M and S.

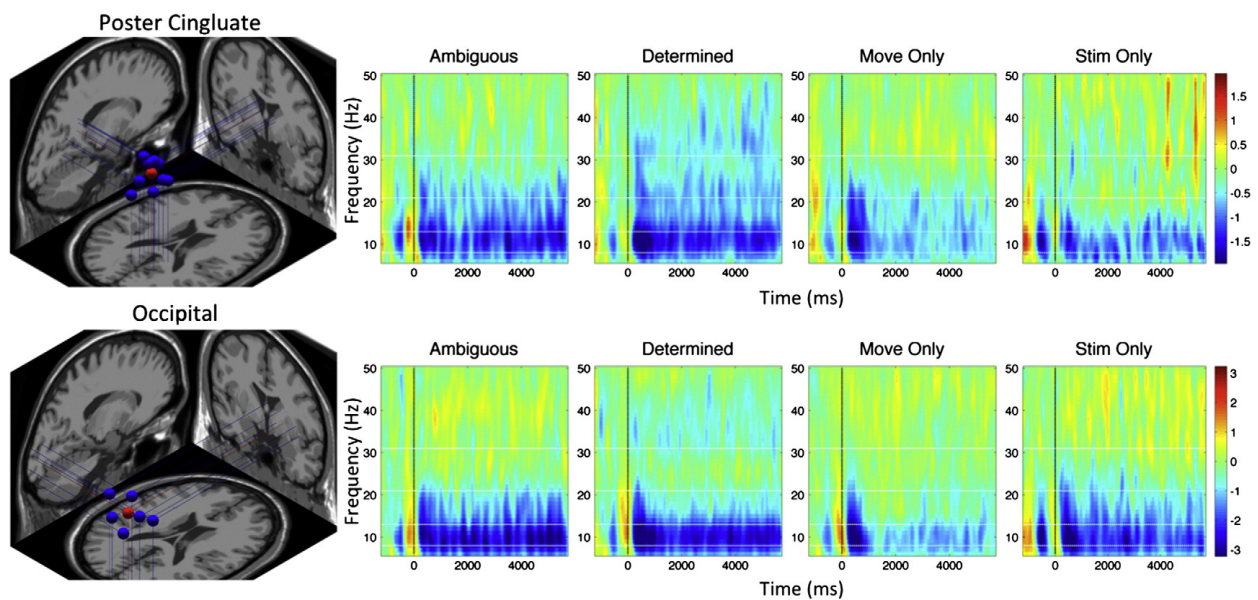


Fig. 4. Task related clusters located in the posterior cingulate and right occipital cortex are shown together with the average time frequency plots for each condition. On the left, spheres representing the equivalent current dipole locations of independent components included in the cluster are projected onto axial, coronal and sagittal MRI slices. On the right, the log power for frequencies in the range from 3 to 50 Hz are shown for each condition in a time window from 1 s before to 6 s after the first onset of the visual stimulus array. Blue colors indicate a decrease in oscillatory power from the pre-stimulus period and red colors indicate an increase in oscillatory power. Activity in these areas was characterized by marked desynchronization in the alpha band, particularly for conditions in which an apparent motion stimulus was presented. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2 and Fig. 4). This latter pattern is consistent with the established role of this cortical region in visual processing.

Fig. 5 shows the average event related changes in oscillatory power for the SMC, SPL and MOG clusters. The SMC cluster is characterized by robust alpha and beta band ERD that spans the entire task interval for conditions containing manual rotation of the joystick (A, D and M). In contrast, the S condition, in which no action was performed, was characterized by a clear pattern of alpha band synchrony. The general response pattern of this SMC cluster is compatible with a role in motor related processing, supporting our assertion that it captures contributions from the sensorimotor cortex. The SPL cluster displayed prominent beta band ERD for the A and D compared to the M and S conditions, although only the difference to the S condition was significant. The finding of stronger inferior parietal activity when visual and action are combined is compatible with the general role of this cortical region in visuomotor integration (e.g. Wise et al., 1997). In contrast to the SMC and SPL clusters, the alpha ERD of the middle occipital cluster was more pronounced for conditions that included apparent motion (A, D and S) indicating a putative role for this region in processing of the apparent motion stimuli.

In addition to being task related, the SMC, SPL and MOG clusters also met criterion for classification as priming related. That is, they demonstrated greater ERD in the A than D condition. The results of the statistical analysis are shown in Fig. 6 and Table 2. The bar graphs in Fig. 6 show the ERSP in select frequency bins for each experimental condition averaged over the post-stimulus period (1–5 s). Panel F provides the location of the center of each cluster projected onto a single axial slice of the MNI brain. The top row shows bar plots (A–C) from clusters classified as priming related. The posterior Cing and OCC clusters (panels D–E), although task related, did not display a pattern consistent with a role in action priming of visual perception.

The results of the connectivity analysis are provided in Fig. 7. The number of IC pairs in this analysis was reduced because not all participants contributed an IC to each of the five clusters of interest. Significant differences between conditions were found in four of the cluster pairs. In all cases, difference were in the gamma band and resulted because of greater phase locking in the A compared to the D and M conditions. That is, gamma coupling was greatest when action primed the perception of ambiguous apparent motion compared to when action occurred alone or together with unambiguous apparent motion. This pattern of increased gamma band phase locking was observed between SMC and both the SPL and Cing clusters as well as between the SPL and both the Cing and OCC clusters. The spatial pattern of the coupling broadly traced a dorsal pathway between primary motor and visual areas. Significant difference in phase locking between conditions was not observed in the lower frequency bands.

Discussion

In keeping the findings of Wohlschläger (2000), our results demonstrate that action can prime vision. When viewing ambiguous apparent motion in the absence of an action, participants were equally likely to perceive motion as either clockwise or anti-clockwise. However, when the same ambiguous apparent motion was accompanied by manual rotation, the participants perceived the direction of visual motion as the same as the direction of manual rotation. Thus manual rotation served as an effective prime that disambiguated the direction of perceived motion.

Our EEG results support the hypotheses that priming of visual perception by action is mediated by large-scale neural coupling across the dorsal visual stream, including sensorimotor cortex. Our results showed that action priming resulted in an increase in neural activity in discrete regions of a dorsal visuo-motor processing circuit and a concomitant increase in the large-scale gamma synchrony across this circuit. Component clusters in extrastriate, parietal and sensorimotor cortices showed the greatest activity and the strongest gamma

band synchrony when the participants' action primed the perceived direction of ambiguous motion. These results provide broad support for theories of common coding (Hommel et al., 2001; Prinz, 1997) by demonstrating that the influence of action on perception is mediated over the same general pathway involved in visual to motor integration.

Decreases in alpha and beta band power during task intervals are characteristic of event related desynchronization and serves as an index of localized increases in cortical activity related to aspects of motor (Pfurtscheller and Lopes da Silva, 1999) and visual (Williamson et al., 1997) processing. Clusters of cortical sources were classified according to the pattern of desynchronization across the four experimental conditions. Both the occipital and cingulate clusters showed greater activity in conditions in which action and visual motion occurred together, a pattern of activity suggestive of a role in visual motor integration. The implication that early visual areas play a role in visual-motor processing is consistent with EEG and fMRI findings demonstrating that audio-visual (Doehrmann et al., 2010; Molholm et al., 2002; Romei et al., 2007) and sensorimotor-visual (Merabet et al., 2008) integration influences early visual processing. This result is also compatible with the anatomical evidence of projections from parietal association areas to striate cortex (Borra and Rockland, 2011) and with the contemporary views that crossmodal interactions occur at earlier processing stages than previously assumed.

The posterior cingulate responds to sensory stimuli and is involved in spatial orientation and memory (Vogt et al., 1992). Functionally, this area may be involved in monitoring the relationship between sensory events and one's own behavior (Vogt et al., 1992) or in deploying spatial attention based on a cue or anticipation (Mesulam et al., 2001; Small et al., 2003). In the present experiment, therefore, the increase in activity in posterior cingulate may reflect greater spatial cueing or an increase in visuospatial attention to the apparent motion display. Interestingly our findings imply that the concurrent action enhances this process, possibly owing to overlapping spatial features of the action and perception. It should be pointed out, however, that the posterior cingulate was not one of the brain areas we originally anticipated and its proposed role in the present task is speculative.

More relevant to the current study is the finding that the sensorimotor cortex, the superior parietal lobe and extrastriate cortex in the middle occipital gyrus demonstrated a pattern of activity consistent with a role in the priming of perception by action. These areas all showed the greatest activity when action primed or disambiguated visual perception. Event related desynchronization in the primary motor and superior parietal clusters was greatest for the three action conditions, and weakest in the vision only condition, emphasizing the role of the motor and parietal regions in motor execution and sensorimotor transformation respectively (Rizzolatti and Luppino, 2001). In contrast, desynchronization in the middle occipital cluster was strongest in apparent motion conditions and lowest in the movement only condition, when no visual motion was presented. The functional response and the anatomical location of the middle occipital cluster are compatible with human MT/V5, a region well established for its role in the perception of real and apparent motion (e.g. Bartels et al., 2008; Corbetta, 1990; Goebel et al., 1998; Muckli et al., 2002).

Activity in extrastriate and parietal regions was significantly greater when action aided in determining the perceived direction of ambiguous apparent motion. Moreover, gamma band phase locking, an indication of functional connectivity, was also greatest between motor, parietal and extrastriate regions when action influenced apparent motion. Both area MT and parietal cortex play a role in establishing and switching between multistable perceptual states (Sterzer et al., 2009) induced by ambiguous apparent motion displays and multistable perceptions (Sterzer and Rees, 2008). For example, the level of activity in parietal cortex (LIP) and MT prior to the onset of an ambiguous apparent motion stimulus predicts the perceived direction of motion (Williams et al., 2003). In addition, Merchant et al. (2005) found that the detection of

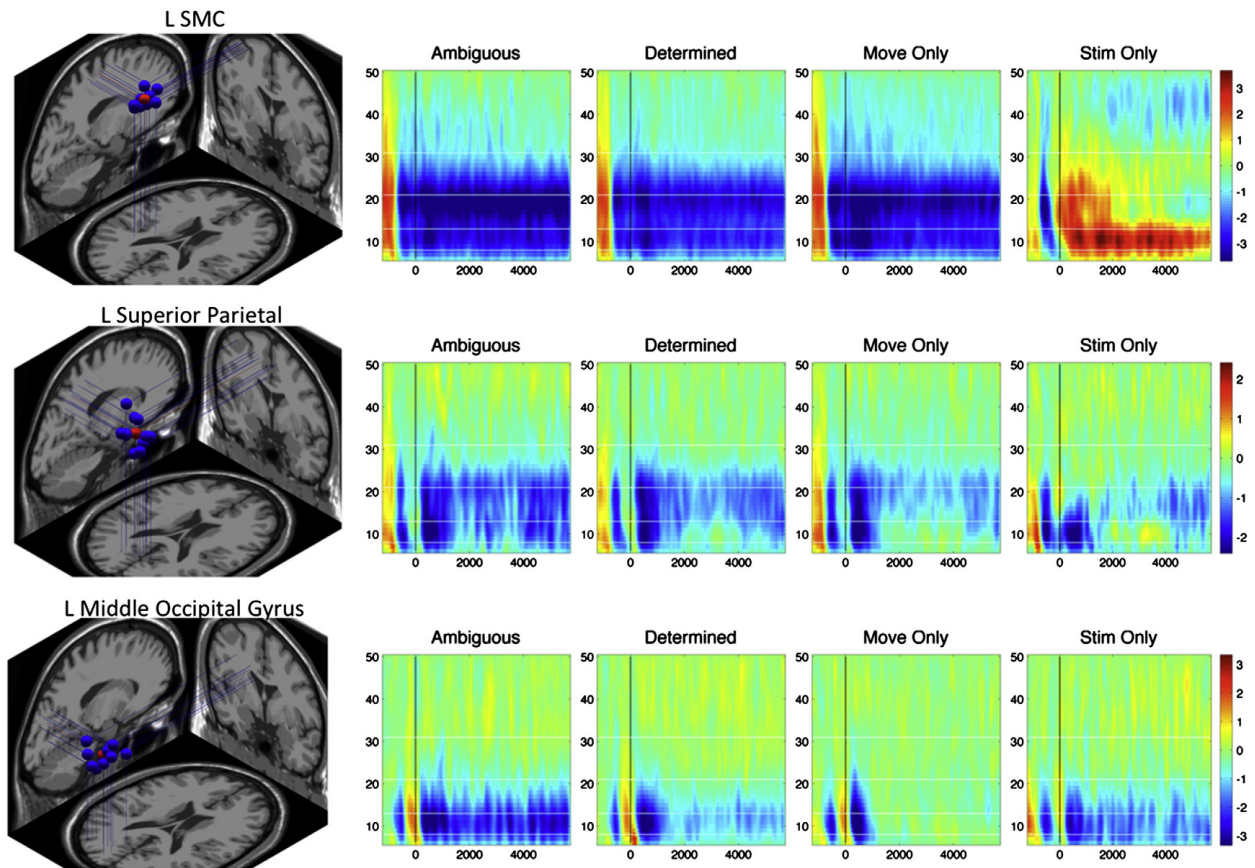


Fig. 5. Priming related clusters located in the left precentral gyrus, superior parietal lobe and middle occipital gyrus are shown together with the average time frequency plots for each condition. On the left, spheres representing the equivalent current dipole locations of independent components included in the cluster are projected onto axial, coronal and sagittal MRI slices. On the right, the log power for frequencies in the range from 3 to 50 Hz are shown for each condition in a time window from 1 s before to 6 s after the first onset of the visual stimulus array. Blue colors indicate a decrease in oscillatory power from the pre-stimulus period and red colors indicate an increase in oscillatory power. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

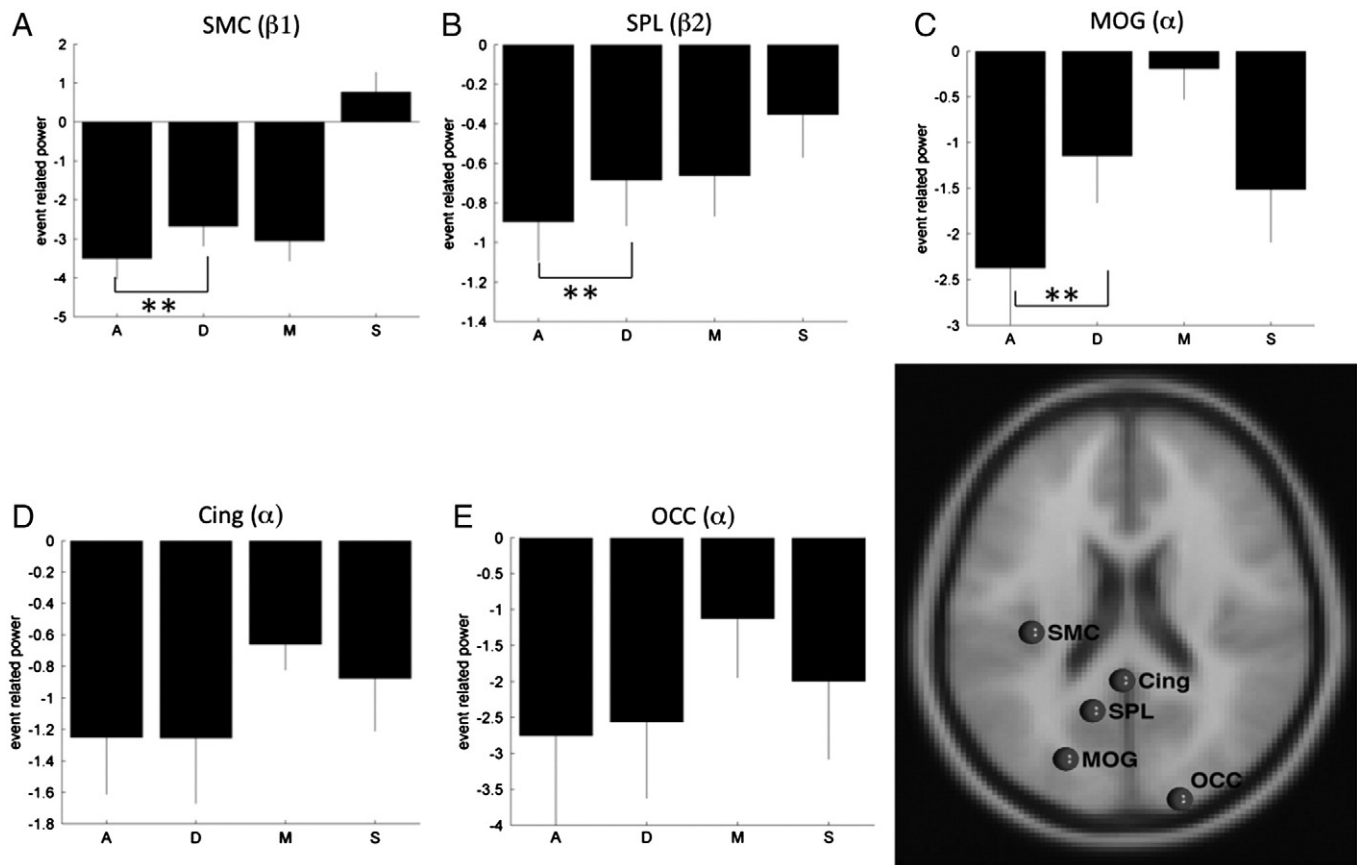


Fig. 6. Event related changes in power in select frequency bands are shown for priming (A–C) and task related (D,E) clusters averaged across the interval from 1 to 5 s following the first onset of the visual stimulus array. Double asterisks identify clusters in which desynchronization was significantly greater in the ambiguous apparent motion condition compared to the determined condition. (F) The central location of each of the cluster is projected onto a single axial MRI slice. Error bars represent standard error. (SMC: Sensorimotor cortex; SPL: superior parietal lobe; MOG: middle occipital gyrus; Cing: posterior cingulate; OCC: occipital cortex).

path guided apparent motion was correlated with correct reconstruction of the path by neurons in posterior parietal cortex. Williams et al. (2003) suggest that when viewing ambiguous apparent motion, medial temporal cortex (MT, MST) may provide a non-directional representation of movement, whereas lateral intraparietal sulcus codes for or “interprets” the perceived direction of motion.

The proposed interdependence between these areas in determining the direction of apparent motion is compatible with our finding of increased gamma band coupling. The phase locking analysis revealed an increase in gamma coupling among sensorimotor, extrastriate and parietal sources when action successfully primed apparent motion. A similar increase in gamma coupling between bilateral MT facilitates the emergence of coherent motion perception from apparent motion across the retinal midline (Rose and Büchel, 2005). In the current experiment, neural coherence in the gamma band may facilitate efficient visuo-motor integration by dynamically linking neural populations into functional groups (Womelsdorf and Fries, 2006) and consequently biasing the interpretation of the apparent motion display to be compatible with ongoing action. The perception of ambiguous visual stimuli is influenced by the neural state of extrastriate processing areas at the onset of the visual stimulus (Pearson and Brascamp, 2008; Sterzer et al., 2009). In the present case, manual rotation may influence activity in parietal and extrastriate regions to prime the perceived direction of motion. Recent evidence suggests that this influence may also extend from MT to V1 (Wibral et al., 2009).

The present data are compatible with the Ideomotor hypotheses that actions are represented by their perceived consequences (see Shin et al., 2010 for a recent review) and that action and perception share a common neural code (Hommel et al., 2001; Prinz, 1997;

Schütz-Bosbach and Prinz, 2007). Ideomotor theories propose that a single representation underlies action planning, imagination, execution as well as the perception of action and its consequences (Shin et al., 2010). Thus, although our results are specific to action execution, theory predicts that similar results should emerge if participants are simply asked to imagine or plan actions. In support, Wohlschläger (2000) showed that action planning was sufficient for priming the perceived direction and an ambiguous apparent motion stimulus. Demonstration that increases in visuo-motor coupling similar to that shown in the present study are generated during motor imagination or preparation would provide further general support for the ideomotor hypothesis. The current results are also compatible with the notion that the expectation of performing a movement provides top down modulation on parietal and temporal visual areas similar to that described by Sterzer et al. (2009). Nonetheless, our phase locking results suggest that this expectation involves, at least in part, increased functional connectivity of motor cortex suggesting a possible homology between expectations and motor planning/execution.

Conclusion

Our results provide general support for theories of common coding and further suggest that visual and motor codes may be represented and influenced by gamma coupling across multiple discrete neural ensembles along the dorsal visual stream linking vision to action. Vision is a constructive process that often requires disambiguation of impoverished visual input. We have illustrated how action may play a role in disambiguating vision by creating a bias toward a one of many possible percepts. These data demonstrate that action influences perception by strengthening the interaction across a broad

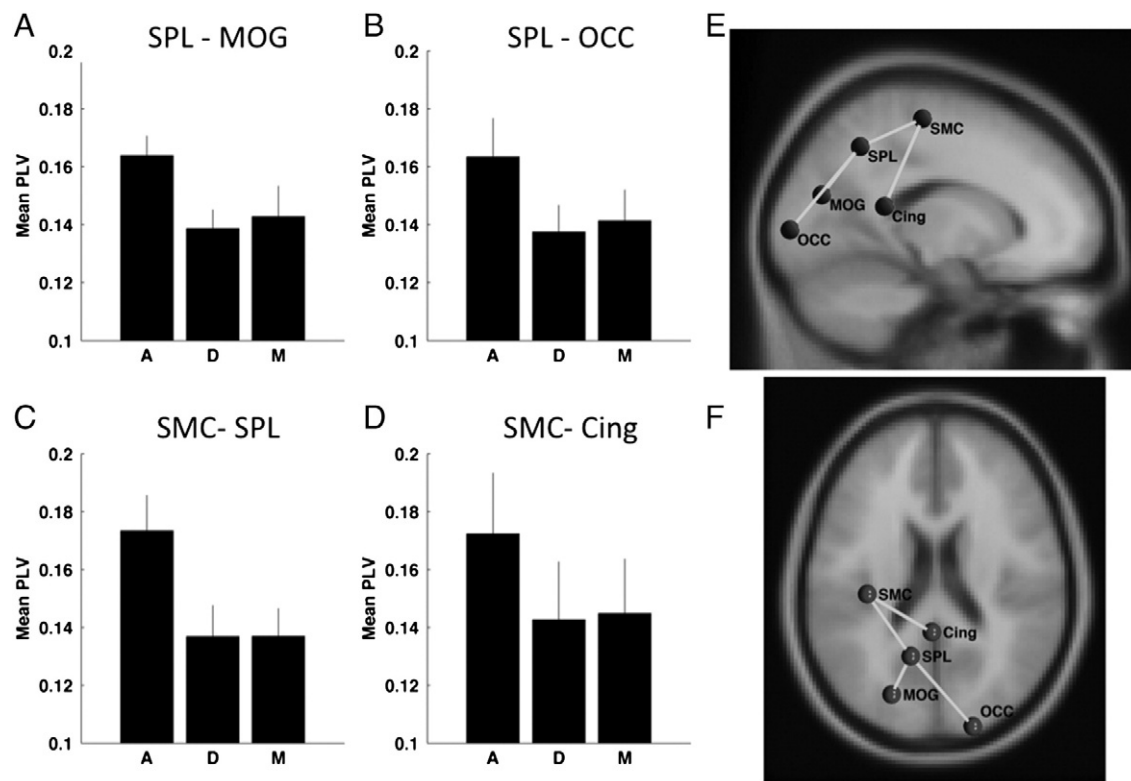


Fig. 7. The gamma band phase locking value is shown for cluster pairs in which the phase locking was significantly greater during the Ambiguous compared to the Determined and Motor only conditions. The panels on the left show the relative locations of the center of the task and priming related clusters projected onto mid sagittal (E) and mid axial (F) slices. The lines connect cluster pairs demonstrating greater gamma phase locking for the ambiguous condition. (SMC: Sensorimotor cortex; SPL: superior parietal lobe; MOG: middle occipital gyrus; Cing: posterior cingulate; OCC: occipital cortex).

sensorimotor network, for the putative purpose of integrating compatible action outcomes and sensory information into a single coherent percept. In the present study participants were more likely to perceive motion as similar to their action. However, in addition to this assimilation effect, participants may also demonstrate contrast in which they are less sensitive to a similar action (Grosjean et al., 2009). Investigating the neural dynamics underlying these effects may provide greater insight into the relationship between gamma band coupling and the bidirectional influence between vision and action.

Acknowledgments

Parts of this research was supported by a summer research grant awarded to K.J.J. by Research and Sponsored Programs at WWU. We would also like to thank all those who contributed to the collection and analysis of data.

References

Astafiev, S.V., Stanley, C.M., Shulman, G.L., Corbetta, M., 2004. Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nat. Neurosci.* 7, 542–548.

Bartels, A., Logothetis, N.K., Moutoussis, K., 2008. fMRI and its interpretations: an illustration on directional selectivity in area v5/MT. *Trends Neurosci.* 31 (9), 444–453.

Behmer, L.P., Jantzen, K.J., 2011. Reading sheet music facilitates sensorimotor mu-desynchronization in musicians. *Clin. Neurophysiol.* 122, 1342–1347.

Blaesi, S., Wilson, M., 2010. The mirror reflects both ways: action influences perception of others. *Brain Cogn.* 72, 306–309.

Blakemore, S., Frith, U., 2005. The learning brain: lessons for education: a précis. *Dev. Sci.* 8, 459–465.

Borra, E., Rockland, K.S., 2011. Projections to early visual areas V1 and V2 in the calcarine fissure from parietal association areas in the macaque. *Front. Neuroanat.* 5, 35.

Bressler, S.L., Kelso, J.A.S., 2001. Cortical coordination and cognition. *Trends Cogn. Sci.* 5, 26–36.

Cattaneo, L., Barchiesi, G., Tabarelli, D., Arfeller, C., Sato, M., Glenberg, A.M., 2010. One's motor performance predictably modulates the understanding of others' actions through adaptation of premotor visuo-motor neurons. *Soc. Cogn. Affect. Neurosci.* 6, 301–310.

Cheyne, D., Bakhtazad, L., Gaetz, W., 2006. Spatiotemporal mapping of cortical activity accompanying voluntary movements using an event-related beamforming approach. *Hum. Brain Mapp.* 27, 213–229.

Corbetta, M., Miezin, F.M., Dobmeyer, S., Shulman, G.L., Petersen, S.E., 1990. Attentional modulation of neural processing of shape, color, and velocity in humans. *Science* 248, 1556–1559.

Craigheo, L., Fadiga, L., Umiltà, C., Rizzolatti, G., 1999. Action for perception: a motor-visual attentional effect. *J. Exp. Psychol. Hum.* 25, 1673–1692.

Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Methods* 134, 9–21.

Doehrmann, O., Weigelt, S., Altmann, C.F., Kaiser, J., Naumer, M.J., 2010. Audiovisual functional magnetic resonance imaging adaptation reveals multisensory integration effects in object-related sensory cortices. *J. Neurosci.* 30, 3370–3379.

Doesburg, S.M., Roggeveen, A.B., Kitajo, K., Ward, L.M., 2008. Large-scale gamma-band phase synchronization and selective attention. *Cereb. Cortex* 18, 386–396.

Doesburg, S.M., Green, J.J., McDonald, J.J., Ward, L.M., 2009. From local inhibition to long-range integration: a functional dissociation of alpha-band synchronization across cortical scales in visuospatial attention. *Brain Res.* 1303, 97–110.

Gibson, J.J., 1979. *The Ecological Approach to Visual Perception*. Houghton Mifflin, Boston.

Goebel, R., Khorram-Sefat, D., Muckli, L., Hacker, H., Singer, W., 1998. The constructive nature of vision: direct evidence from functional magnetic resonance imaging studies of apparent motion and motion imagery. *Eur. J. Neurosci.* 10, 1563–1573.

Goodale, M.A., Milner, A.D., 1992. Separate visual pathways for perception and action. *Trends Neurosci.* 15, 20–25.

Goodale, M.A., Westwood, D.A., 2004. An evolving view of duplex vision: separate but interacting cortical pathways for perception and action. *Curr. Opin. Neurobiol.* 1, 203–211.

Grosjean, M., Zwickel, J., Prinz, W., 2009. Acting while perceiving: assimilation precedes contrast. *Psychol. Res.* 73, 3–13.

Hamilton, A., Wolpert, D.M., Frith, U., 2004. Your own action influences how you perceive another person's action. *Curr. Biol.* 14, 493–498.

Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., Rizzolatti, G., 1998. Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proc. Natl. Acad. Sci. U. S. A.* 95, 15061–15065.

Hommel, B., Müsseler, J., Aschersleben, G., Prinz, W., 2001. The theory of event coding (TEC): a framework for perception and action planning. *Behav. Brain Sci.* 24, 849–878.

James, W., 1890. *The Principles of Psychology*. Cossimo Classics, New York, NY. (reprint 2007).

- Kakei, S., Hoffman, D.S., Strick, P.L., 1999. Muscle and movement representations in the primary motor cortex. *Science* 285, 2136–2139.
- Lachaux, J.P., Rodriguez, E., Martinerie, J., Varela, F.J., 1999. Measuring phase synchrony in brain signals. *Hum. Brain Mapp.* 8, 194–208.
- Lindemann, O., Bekkering, H., 2009. Object manipulation and motion perception: evidence of an influence of action planning on visual processing. *J. Exp. Psychol. Hum.* 35, 1062–1071.
- Merabet, L.B., Hamilton, R., Schlaug, G., Swisher, J.D., Kiriakopoulos, E.T., Pitskel, N.B., Kauffman, T., Pascual-Leone, A., 2008. Rapid and reversible recruitment of early visual cortex for touch. *PLoS One* 3 (8).
- Merchant, H., Battaglia-Mayer, A., Georgopoulos, A.P., 2005. Decoding of path-guided apparent motion from neural ensembles in posterior parietal cortex. *Exp. Brain Res.* 161 (4), 532–540.
- Mesulam, M.M., Nobre, A.C., Kim, Y.H., Parrish, T.B., Gitelman, D.R., 2001. Heterogeneity of cingulate contributions to spatial attention. *NeuroImage* 13 (6), 1065–1072.
- Molholm, S., Ritter, W., Murray, M.M., Javitt, D.C., Schroeder, C.E., Foxe, J.J., 2002. Multisensory auditory–visual interactions during early sensory processing in humans: a high-density electrical mapping study. *Cogn. Brain Res.* 14, 115–128.
- Muckli, L., Kriegeskorte, N., Lanfermann, H., Zanella, F.E., Singer, W., Goebel, R., 2002. Apparent motion: event-related functional magnetic resonance imaging of perceptual switches and states. *J. Neurosci.* 22, 1–5.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9, 97–113.
- Onton, J., Delorme, A., Makeig, S., 2005. Frontal midline EEG dynamics during working memory. *NeuroImage* 27, 341–356.
- Oostenveld, R., Praamstra, P., 2001. The five percent electrode system for high-resolution EEG and ERP measurements. *Clin. Neurophysiol.* 112, 713–719.
- Pearson, J., Brascamp, J., 2008. Sensory memory for ambiguous vision. *Trends Cogn. Sci.* 12, 334–341.
- Pfurtscheller, G., Lopes da Silva, F.H., 1999. Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clin. Neurophysiol.* 110, 1842–1857.
- Prinz, W., 1997. Perception and action planning. *Eur. J. Cogn. Psychol.* 9, 129–154.
- Rizzolatti, G., Craighero, L., 2004. The mirror–neuron system. *Neuroscience* 27, 169–192.
- Rizzolatti, G., Luppino, G., 2001. The cortical motor system. *Neuron* 31, 889–901.
- Rizzolatti, G., Matelli, M., 2003. Two different streams form the dorsal visual system: anatomy and functions. *Exp. Brain Res.* 153, 146–157.
- Romei, V., Murray, M., Merabet, L.B., Thut, G., 2007. Occipital transcranial magnetic stimulation has opposing effects on visual and auditory stimulus detection: implications for multisensory interactions. *J. Neurosci.* 27, 11465–11472.
- Rose, M., Büchel, C., 2005. Neural coupling binds visual tokens to moving stimuli. *J. Neurosci.* 25, 10101–10104.
- Rueschemeyer, S.A., Lindemann, O., van Elk, M., Bwektering, H., 2009. Embodied cognition: the interplay between automatic resonance and selection-for-action mechanisms. *Eur. J. Soc. Psychol.* 39, 1180–1187.
- Schütz-Bosbach, S., Prinz, W., 2007. Perceptual resonance: action-induced modulation of perception. *Trends Cogn. Sci.* 11, 349–355.
- Senkowski, D., Schneider, T.R., Foxe, J.J., Engel, A.K., 2008. Crossmodal binding through neural coherence: implications for multisensory processing. *Trends Neurosci.* 31, 401–409.
- Shin, Y., Proctor, R., Capaldi, E., 2010. A review of contemporary ideomotor theory. *Psychol. Bull.* 136, 943–974.
- Singer, W., Gray, C.M., 1995. Visual feature integration and the temporal correlation hypothesis. *Annu. Rev. Neurosci.* 18, 555–586.
- Small, D.M., Gregory, M.D., Mak, Y.E., Gitelman, D., Mesulam, M.M., Parrish, T., 2003. Dissociation of neural representation of intensity and affective valuation in human gustation. *Neuron* 39, 701–711.
- Sterzer, P., Rees, G., 2008. A neural basis for percept stabilization in binocular rivalry. *J. Cogn. Neurosci.* 20, 389–399.
- Sterzer, P., Kleinschmidt, A., Rees, G., 2009. The neural bases of multistable perception. *Trends Cogn. Sci.* 13, 310–318.
- Varela, F., Lachaux, J.P., Rodriguez, E., Martinerie, J., 2001. The brainweb: phase synchronization and large-scale integration. *Nat. Rev. Neurosci.* 2, 229–239.
- Vogt, B.A., Finch, D.M., Olson, C.R., 1992. Functional heterogeneity in cingulate cortex: the anterior executive and posterior evaluative regions. *Cereb. Cortex* 2, 435–443.
- Ward, L.M., Doesburg, S.M., 2009. Synchronization analysis in EEG and MEG. In: Handy, T.C. (Ed.), *Brain Signal Analysis*. The MIT Press, Cambridge, MA, pp. 171–204.
- Ward, L.M., MacLean, S.E., Kirschner, A., 2010. Stochastic resonance modulates neural synchronization within and between cortical sources. *PLoS One* 5 (12), e14371, <http://dx.doi.org/10.1371/journal.pone.0014371>.
- Wibral, M., Bledowski, C., Kohler, A., Singer, W., Muckli, L., 2009. The timing of feedback to early visual cortex in the perception of long-range apparent motion. *Cereb. Cortex* 19, 1567–1582.
- Williams, Z.M., Elfar, J.C., Eskandar, E.N., Toth, L.J., Assad, J.A., 2003. Parietal activity and the perceived direction of ambiguous apparent motion. *Nat. Neurosci.* 6, 616–623.
- Williamson, S.J., Kaufman, L., Lu, Z.L., Wang, J.Z., Karron, D., 1997. Study of human occipital alpha rhythm: the alphon hypothesis and alpha suppression. *Int. J. Psychophysiol.* 26, 63–76.
- Wise, S.P., Boussaoud, D., Johnson, P.B., Caminiti, R., 1997. Premotor and parietal cortex: corticocortical connectivity and combinatorial computations. *Annu. Rev. Neurosci.* 20, 25–42.
- Wohlschläger, A., 2000. Visual motion priming by invisible actions. *Vis. Res.* 40, 925–930.
- Womelsdorf, T., Fries, P., 2006. Neuronal coherence during selective attentional processing and sensory–motor integration. *J. Physiol. Paris* 100, 182–193.
- Zwivel, J., Prinz, W., 2012. Assimilation and contrast: the two sides of specific interference between action and perception. *Psychol. Res.* 76, 171–182.