**Title Page**

**Title: Increasing interhemispheric connectivity between human visual motion areas uncovers asymmetric sensitivity to horizontal motion**

**Running Title:** Asymmetric interhemispheric connectivity in human motion areas

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**Summary**

Our conscious perceptual experience relies on a hierarchical process involving integration of low-level sensory encoding and higher-order sensory selection[1]. This hierarchical process may scale at different levels of brain functioning, including integration of information between the hemispheres[2–5]. Here, we test this hypothesis for the perception of visual motion stimuli. Across 3 experiments, we manipulated the connectivity between the left and right visual motion complex (V5/MT+) responsible for horizontal motion perception[2,5] by means of transcranial magnetic stimulation (TMS)[6,7]. We found that enhancing the strength of connections from the left to the right V5/MT+, by inducing spike-timing-dependent plasticity[8] in this pathway, increased sensitivity to horizontal motion. These changes were present immediately and lasted at least 90 minutes after intervention. Notably, little perceptual changes were observed when strengthening connections from the right to the left V5/MT+. Furthermore, we found that this asymmetric modulation was mirrored by an asymmetric perceptual bias in the direction of the horizontal motion. Overall, observers were biased towards leftwards relative to rightward motion direction. Crucially, following the strengthening of the connections from right to left V5/MT+, this bias could be momentarily reversed. These results suggest that the projections connecting left and right V5/MT+ in the human visual cortex are asymmetrical, subtending a hierarchical role of hemispheric specialization[9–12] favoring left to right hemisphere processing for integrating local sensory input into coherent global motion perception.

**Results**

The apparent motion quartet is an ambiguous stimulus consisting of a pair of dots that flash alternately at the two diagonals of an invisible square[1]. The two dots are perceived to move backward and forward along the horizontal or vertical edges of the square. The direction of this illusory movement relies on the relative separation of the dots in the horizontal and vertical directions. By keeping the horizontal separation constant and manipulating the vertical separation, it is possible to identify the aspect ratio that creates equal proportions of horizontal and vertical motion perception, referred to as the parity ratio (PR). PR is a behavioral measure associated with interhemispheric communication between areas subserving motion perception[5]. One candidate area for the perception of motion is the human V5/MT+ area[13,14] (hereinafter referred to as V5).

Here, in a first experiment (Experiment-1), we examined whether we could selectively potentiate the physiological connectivity in the V5-V5 interhemispheric pathway, and thus enhance sensitivity to horizontal motion as indexed by the PR of the apparent motion quartet. We first determined each individual's PR during perception of the motion quartet, then re-tested PR again before (baseline), and four times (0, 30, 60, 90 minutes) after a TMS protocol comprising repeated asynchronous paired stimulation of left V5 (lV5) and right V5 (rV5), in order to modulate the strength of the pathway connecting the targeted areas (SI). This TMS protocol based upon Hebbian principles[8,15], referred to as cortico-cortical paired associative stimulation (ccPAS)[6,16–18], mimics neuronal stimulation known to induce spike-timing-dependent plasticity (STDP). We applied 90 paired pulses over lV5 and rV5 at 0.1Hz[6,7,19–22] in 15 healthy volunteers who participated in four ccPAS conditions. The temporal pattern and stimulation procedures of the ccPAS intervention varied across the four conditions.

In a critical condition, namely lV5-rV5 ccPAS, each TMS pulse over lV5 was followed by a pulse over rV5. In this way, activation spread induced by the first stimulation over lV5 (i.e., the 'pre-synaptic' node according to the Hebbian rule) could preactivate, via transcallosal communication, the contralateral area rV5 (i.e., the 'post-synaptic' node) just before delivery of the second pulse over that area. This coupling of pre- and post-synaptic activity is optimal for inducing STDP and thus strengthening the lV5-rV5 pathway[8,16]. In a second critical condition, i.e., rV5-lV5 ccPAS, we delivered TMS in the reverse order of stimulation, i.e., applying the first paired pulse over rV5 and the second pulse over lV5. In both conditions, the inter-pulse interval (IPI) was set to 25ms, based on the timing of interhemispheric communication[2,23]. According to the communication through coherence framework[24,25], this IPI, corresponding to 40 Hz oscillatory activity, is critical to create convergent activation in the 'post-synaptic' node of the V5-V5 route and thus elicit Hebbian-like plasticity[25,26]. In a control condition (V5&V5_t0), we tested whether ccPAS effects result from temporally precise activations that induces STDP[8,16]. To this aim, we applied exactly the same number of pulses over left and right V5 but with a 0 ms interval, which does not induce the same sequence of pre- and post-synaptic activation and thus is expected not to induce STDP. Finally, in a further control condition (lV5-rV5_sham), lV5-rV5 ccPAS was delivered with 25ms IPI but in sham mode, controlling for nonspecific TMS effects (Figure 1A).

To examine if potentiation of physiological connectivity in the V5-V5 cortico-cortical pathway leads to a threshold change in the relative weighting of horizontal and vertical motion perception, we contrasted PR values in the four ccPAS conditions of Experiment-1 before and four times after ccPAS. Reduced PR values suggest an enhanced sensitivity for horizontal over vertical motion. The contrast between the PR values recorded at the four ccPAS conditions and four times after the intervention revealed that ccPAS altered the PR values recorded after the intervention ($F_{12,168}$=3.12, p<0.001; $\eta^2_p$=0.18). Specifically, we demonstrated that lV5-rV5 ccPAS had a sustained significant impact on PR values ($F_{4,56}$=3.98, p=0.006; $\eta^2_p$=0.22). PR decreased immediately, as well as 60 and 90 minutes after treatment (all ps<0.017, *Cohen's d*>0.45), whereas no significant PR changes from baseline were observed after 30 minutes of stimulation ($t_{14}$=2.04; p=0.33). In contrast, only a moderate PR decrease was observed after rV5-lV5 ccPAS ($F_{4,56}$=2.54, p=0.05; $\eta^2_p$=0.15), restricted to 30 minutes after stimulation ($t_{14}$=2.75; p=0.036, *Cohen's d*=0.47) (Figure 1B). Direct analysis between lV5-rV5 and rV5-lV5 ccPAS confirms a distinctive stimulation effect across the timepoints ($F_{3,42}$=3.21, p=0.032; $\eta^2_p$=0.19), differing immediately (p=0.044, *Cohen's d*=0.75) and 90 minutes (p=0.029, *Cohen's d*=0.83) after stimulation (see also Table S2). These findings support a more sustained effect of lV5-rV5 ccPAS compared to that of rV5-lV5 ccPAS, under these stimulus and task conditions. Horizontal motion is supported by the integration of local features from both hemispheres into a global percept; this global integration has been associated with increased inter-hemispheric neural coupling in the visual cortex[2,3]. Individuals with lower PR values in the motion quartet exhibit larger diameter axons and faster conduction velocities in the V5-V5 pathway, suggesting that the strength of this pathway might determine sensitivity to horizontal motion[5]. Thus, results of Experiment-1 extend previous correlational evidence by showing that strengthening V5-V5 interhemispheric communication causally facilitates subjective perception of horizontal movement in the motion quartet.

Hebbian plasticity depends on temporally precise activation of pre- and post-synaptic neurons. If augmentation of horizontal motion sensitivity is due to Hebbian-like strengthening of a specific corticocortical pathway, then changing the timing of lV5 and rV5 TMS to a non-optimal interval should not lead to the same PR changes. Indeed, there was no evidence of PR changes following V5&V5_t0 ccPAS. Similarly, no PR changes were observed after lV5-rV5_sham ccPAS (all ps>0.16) (Figure 1B), thus confirming that only ccPAS aimed at modulating the strength of V5-V5 connectivity selectively affected motion perception.

Interestingly, Experiment-1 shows that neurons in the lV5-rV5 pathway were more amenable to physiological potentiation than their counterpart rV5-lV5 neurons. This begs the question of whether the functional asymmetry is merely driven by a distinctive role of rV5 *versus* lV5 in horizontal motion perception, or whether such asymmetry is mainly rooted in V5-V5 connectivity. In two control experiments (Figure S1), we used continuous theta burst stimulation (cTBS) to interfere with the activity of either rV5 or left V5, or both simultaneously. Results suggest that conscious experience of the motion quartet arguably reflects the process of integration of information across the two

hemispheres into a global horizontal motion percept; moreover, augmentation of horizontal motion sensitivity found in Experiment-1 is not simply due to a distinctive functional role of the right as opposed to left V5 *per se*, but to enhanced cortico-cortical connectivity of the lV5-rV5 interhemispheric pathway.

In Experiment-2 we further interrogated whether an asymmetry in interhemispheric V5-V5 interactions coherent with that found in Experiment-1 could be detected at the functional level by testing whether (leftward) direction bias could be disclosed on a different task – involving apparent horizontal motion stimuli – in the absence of any TMS manipulation. To this aim, a counterphasing Gabor stimulus was presented, inducing horizontal apparent motion to 54 participants (Figure 2A). In this case, the perceptual ambiguity relies on the equal and opposite strengths of leftward and rightward apparent motion contained in the stimulus. Whether it is perceived as moving leftward or rightward on each trial thus depends on the internal brain state at the time of stimulus presentation, rather than the stimulus itself. Therefore, if there is a functional left-right asymmetry in the interhemispheric integration underpinning horizontal motion, we should observe a bias towards leftwards motion. This is what we found. Participants scored -21.8 on average (SE=7.4) on a scale ranging from -100 (leftwards perceived motion on every trial) to 100 (rightwards perceived motion on every trial) showing a significant bias to perceive leftwards motion ($t_{53}$=2.94, p=0.005, *Cohens's d*=0.4) (Figure 2B). Thus, Experiment-2 demonstrated a bias to perceive motion in the leftwards direction, which could reflect a left-right interhemispheric asymmetry reminiscent of what we found in Experiment-1. To directly test dependence of this bias on interhemispheric interactions, in Experiment-3 we causally manipulate the strength of interhemispheric V5-V5 connectivity in the direction opposite to the bias. Thus, we administered a rV5-lV5 ccPAS protocol in a subsample of 17 participants from Experiment-2, and presented the Gabor patterns to assess apparent motion in four sessions: two before the ccPAS, one immediately after the intervention and one 30 minutes after the intervention (Figure 2A). We first tested if the leftwards perceptual bias was consistent across sessions regardless of stimulation across Experiment-2 (mean=-21.6; SE=4.2) and the first (mean=-16.1; SE=5.8) and second (mean=-18.5; SE=4.4) sessions before the ccPAS intervention (p>0.05), verifying that the leftwards bias is a stable trait. The contrast between the perceptual scores recorded before the right-to-left ccPAS, immediately (mean=10.5; SE=6.2) and 30 minutes (mean=-2.2; SE=6.6) after the intervention revealed a change in perceptual scores following the ccPAS intervention ($F_{3,48}$=6.4, p<0.001; $\eta_p^2$=0.29). Specifically, immediately after right-to-left ccPAS the leftwards perceptual bias reversed and participants experienced a shift towards rightwards motion (ps<0.003, *Cohen's d*=1.07). We also tested perceptual bias 30 minutes after the intervention and failed to find perceptual bias to either the right or the left direction (Figure 2C).

**Discussion**

Repeated paired stimulation of left followed by right V5 (i.e., lV5-rV5 ccPAS) in Experiment-1 augmented horizontal motion sensitivity expressed during the subjective experience of a visual motion stimulus. These functional changes in the V5-V5 interhemispheric pathway were present immediately, and again 60 and 90 minutes after stimulation. However, when right V5 was stimulated prior to left V5 (rV5-lV5 ccPAS), the alteration of subjective motion sensitivity was limited to 30 minutes after the intervention. These novel results reveal that interhemispheric projections between left and right V5 are functionally relevant to horizontal motion perception, and, intriguingly, asymmetrical in their malleability. Specifically, decreased PR after ccPAS suggests increased interhemispheric communication between the two V5 areas, dominantly when the direction of the stimulation goes from lV5 to rV5. This striking asymmetry in V5-V5 connections found in Experiment-1 was further supported by a leftwards perceptual bias in apparent motion of counterphasing Gabor patterns (Experiment-2), that was attenuated by ccPAS when the direction of stimulation was opposite to such bias (i.e., rV5-lV5 ccPAS; Experiment-3).

Despite V5 receptive fields tend to be large, and can extend across the vertical meridian[27], V5 sensitivity is much higher for contralateral motion stimuli[28], suggesting that interhemispheric transfer between the two V5 is instrumental to perception of horizontal motion for centrally presented stimuli[4]. In keeping, the route between left and right human V5 has been linked to processing of bistable apparent-motion and, interestingly, studies have shown that the strength of connectivity in the V5-V5 pathway is associated with reduced PR in the motion quartet, indexing enhanced horizontal motion sensitivity[5]. Expanding this prior correlational evidence, in Experiment-1 we demonstrate that V5-V5 ccPAS delivered at rest reduces PR in the motion quartet, thus showing a causal role of the interhemispheric V5-V5 pathway in the subjective experience of horizontal apparent-motion[5]. Thus, by showing that manipulation of the strength of V5-V5 connectivity reduces PR, we demonstrate that the V5-V5 pathway is functionally relevant to binding of motion cues across the left and right visual field, thus shaping the conscious experience of the motion quartet.

However, rV5-lV5 ccPAS appeared weaker in inducing this functional modulation relative to lV5-rV5 ccPAS. Our findings suggest that lV5-rV5 more than rV5-lV5 connections are responsive to plastic boosting of horizontal motion perception, demonstrating novel evidence of functional asymmetries in the interhemispheric cortico-cortical pathway connecting the two human motion complexes. Asymmetrical organization of neural networks is a dominant feature of the brain present in the visual and other cortical areas that supports functional specificity[9]. An asymmetric organization of the interhemispheric V5-V5 pathway is strongly supported by electrophysiological evidence of faster callosal transfer of motion information from left to right *versus* right to left visual cortices in humans[29]. Moreover, while both V5 areas show maximal sensitivity to contralateral motion[28], studies have reported that rV5 shows more sensitivity to ipsilateral motion than lV5[30,31], suggesting privileged access to motion information from lV5 via facilitated transcallosal communication. The asymmetry appears also in keeping with the notion that right hemisphere plays a prominent role in global processing[10,12,32,33] (for a review on visual perceptual asymmetries see[34]) and may thus reflect

functional specialization. According to this, during horizontal motion perception visual information is processed hierarchically, beginning with the extraction of local features in both hemispheres[11,35], followed by integration into a global percept mainly in the right hemisphere[10,12,32–34]. Yet, while our findings support an asymmetrical transcallosal communication between the two V5 areas[29], they suggest that conscious experience of horizontal (apparent) motion across hemifiels critically depends on information exchange between both V5 areas, rather than on a unique role of rV5. Indeed, perception of horizontal motion was also enhanced following rV5-to-lV5 ccPAS – which comprises the same amount of rV5 and lV5 stimulation as the lV5-rV5 ccPAS, but differs in their temporal patterning, leading to enhanced V5-V5 communication in the opposite direction, i.e., from rV5 to lV5.

Further support comes from our control experiments showing that cTBS on either lV5 or rV5 alone did not alter processing of apparent-motion; in contrast, cTBS over both lV5 and rV5 increased PR, thus impairing perception of horizontal motion (Figure S1). Thus, although hemispheric specializations could contribute to asymmetries in transcallosal communication, the disparity observed in Experiment-1 is not merely driven by a dominant role of rV5 *versus* lV5 in the conscious experience of the motion quartet, but rather is attributable to asymmetries in the V5-V5 pathway. These findings uncover a distinctive functional role of the lV5-rV5 cortico-cortical pathway in the perception of horizontal motion in the motion quartet task.

Experiment-1 showed a different timeline of the aftereffects of the two critical ccPAS manipulations. According to the principles of Hebbian plasticity[8,15], the firing of presynaptic cells before postsynaptic cells leads to long-term potentiation, whereas the firing of postsynaptic cells before presynaptic cells can induce long-term depression. These changes can express immediately and also sometime after the intervention[19–21,37]. Increased horizontal motion sensitivity mostly observed after lV5-rV5 ccPAS may, therefore, reflect a change in the orthodromic activation of lV5-rV5 projections. Reduction of the PR was present at times zero, 60, and 90 minutes after the intervention, whereas PR changes were not observed 30 minutes after lV5-rV5 ccPAS, which could reflect transient variability in the strength of the effect due to noise. Interestingly, this null effect coincided with the time where the opposite rV5-to-lV5 ccPAS intervention leads to a moderate reduction of PR. Note that, during lV5-rV5 ccPAS the stimulation may induce not only orthodromic activation of lV5-rV5 projections, but also antidromic activation of rV5-lV5 projections. Similarly, the opposite might hold true, i.e., rV5-lV5 ccPAS may induce changes in rV5-lV5 projections orthodromically, as well as in lV5-rV5 projections, antidromically. Thus, variability in expression of PR changes over time might be due to the contribution of both orthodromic and antidromic activations of lV5-rV5 projections.

The functional specificity of the lV5-rV5 pathway in the human visual cortex was further supported by a tendency to perceive leftwards motion in counterphasing Gabor patterns. Crucially, this leftward apparent motion was reversed after rV5-lV5 ccPAS, so that individuals experienced a shift towards rightwards apparent motion. Together these results confirm the functional relevance of the lV5-rV5 connections in the conscious experience of horizontal apparent motion.

Further studies are needed to link individual variability in structural and functional V5-V5 asymmetries to ccPAS-induced changes in motion perception and evaluate the role of attention and visual experience in the conscious experience of horizontal apparent motion. Yet, the convergence of the findings across the experiments presented here, would suggest that effective V5-V5 communication provides a neural mechanism: i) causally relevant to motion perception; ii) sensitive to ccPAS manipulation; iii) possibly responsible or at least contributing to bias in the conscious experience of horizontal motion.

In summary, the pathway between human lV5 and rV5 can be functionally manipulated via exogenous neurostimulation, leading to changes in the subjective experience of apparent motion. lV5-rV5 ccPAS enhances horizontal motion sensitivity, whereas a reversed rV5-lV5 ccPAS results in only moderate, short-lasting changes. This change is the result of the strengthening of the V5-V5 pathway and not a mere interference with this circuit (Figure S1). The patterns are consistent with the notion of STDP[8,36] and with hierarchical models of global visual processing linked to the right hemisphere[12,34]. Our results are in line and might arguably explain a more general mechanism associated with the human tendency to scan the environment from left to right, as well as phenomena such as the mental number line bias[38] and the pseudoneglect[39]. Future further studies should directly investigate these hypotheses. Overall, these findings provide novel mechanistic insights into hierarchical models of neural networks in the human brain.

**STAR METHODS**

**RESOURCE AVAILABILITY**

      **1.**      **Lead Contact**

Further information and requests for resources and data should be directed to and will be fulfilled by the Lead Contact, VR (vincenzo.romei@unibo.it)

      **2.**      **Materials Availability**

The stimuli that support the findings of this study are available at: https://osf.io/tc378/.

      **3.**      **Data and Code Availability**

The original datasets and code generated during this study have been deposited to the Open Science Framework (OSF.io) repository available at: https://osf.io/tc378/.

**EXPERIMENTAL MODEL AND SUBJECT DETAILS**

Seventy-one healthy adults took part in the study. Although a few participants took part in more than one experiment, they were naïve with respect to the aims of the study and the stimulation condition delivered (see experiments sections below). All participants had normal or corrected-to-normal vision and none of them had a history of medical, neurological or psychiatric disease. Participants who took part in TMS Experiments-1 and 3, as well as to the control TMS experiments (see SI), were also prescreened as to exclude potential health risks and contraindications associated with brain stimulation. They received a monetary reimbursement of £ 7 per hour. All participants gave written informed consent before taking part in the study, which had been approved by the University of Essex Research Ethics Committee (Ethics number: VR1302) in accordance with the ethical standards of the 1964 Declaration of Helsinki.

**METHOD DETAILS**

**Apparatus**

The tasks and the TMS procedures were performed in a quiet room with the light dimmed. During task execution participants were seated on a comfortable chair and their head was held still by a chin-forehead rest so that the eyes of the participants could be at a distance of 57 cm and centered relative to the screen. Prior to TMS administration (Experiments-1 and 3), participants wore a tight elastic net on the head, with the stimulation spots marked on a micropore tape applied to the net. TMS administration was performed in a separate seat, with the participants' head held by a chin-forehead support minimizing involuntary movements. The TMS coils were borne by mechanical arms and their position was constantly monitored by the experimenter. The intersection of the coil wings was placed directly above the target region. Participants were asked to remain still and relaxed throughout the TMS session.

### Motion quartet task

The motion quartet task was created and displayed using MATLAB (The Mathworks Inc., Natick, USA) environment with the Psychophysics Toolbox 3 extensions [40]. Stimuli were presented on an 18" CRT monitor (ViewSonic G90fB, ViewSonic Corporation, Walnut, USA) with a resolution of 1280 x 1024 pixel and a vertical refresh rate of 85Hz. The quartet stimulus consisted of four white squares (each size, 0.75 x 0.75 degrees of visual angle; from now on expressed as °), displayed in alternation two by two on diagonally opposite corners of an imaginary rectangle (horizontal size, 4.4°) with a white fixation cross (size, 0.27° x 0.27°) in its center. Stimuli were presented on a dark gray background. Such alternation at 4 Hz, results in the perception of the apparent motion by associating couple by couple the squares on the opposite sides of the rectangle leading to a bistable perception of movement either horizontal or vertical.

Since the horizontal distance was fixed between the squares (4.4°), the motion is perceived either horizontally or vertically depending on their vertical distance[41], but not both horizontally and vertically at the time[42,43]. The parity ratio (PR) is the aspect ratio that yields an equal proportion of horizontal and vertical motion percepts. PR is subject to large interindividual variability[4,44], but is a stable intraindividual trait[5]. Following the method used by Genç and collaborators[5], two sequential procedures were used to assess the PR of each participant: the method of limits (MoL) and subsequently the method of constant stimuli (MoCS). In the MoL the vertical distance between the squares varied at every cycle by 5.4 arc min, either diminishing from a vertical distance of 14.63° or increasing from a vertical distance of 1.17°. Participants had to press the space bar key as soon as their perception switched from horizontal to vertical motion and vice versa. There were 20 trials for both conditions, randomly presented. MoL was assessed once per participant, at the beginning of each of the 4 experimental sessions. The PR was accurately calculated with the MoCS task. Observers were presented with eight different aspect ratios, differing by the vertical distance. One was the average vertical distance of perception-switching roughly estimated with the MoL task, the remaining seven were placed around this mean value in steps of 0.88°, with four larger and three smaller than the mean. Every trial consisted of three complete cycles of flashing squares in both diagonal corners (1.5 s); at the end of the sequence, participants reported whether they experienced the squares moving along the vertical or the horizontal axis by pressing two different keys.
Every block consisted of sixteen trials per aspect ratio in randomized order, half of which could start with the squares in two (opposite) corners, the other half in the other corners. Every session consisted of three blocks for 384 trials in total.

### Horizontal motion direction task

This stimulus consists of a counterphasing Gabor, i.e., a vertical sinusoidal grating with a spatial frequency of 1 cycles/degree, modulated by an isotropic Gaussian envelope with a standard deviation of 2.8 degrees, counterphasing at a rate of 3.8 Hz. The phase of the first frame was randomized for each trial. Each stimulus was presented for 1s. Since a counterphasing grating is

mathematically equivalent to the sum of two sinusoids moving in opposite directions, this stimulus creates a bistable perception of movement, with no net motion energy leftwards or rightwards. As in the motion quartet, this task was coded in MATLAB with the Psychophysics Toolbox 3 package and was displayed on the same monitor. Participants were asked to keep their gaze central and respond whether the motion was perceived as leftward or rightward. Each session consisted of 100 trials.

**Experiment-1**

Seventeen volunteers (7 females; mean age 22.6 ± 2.3 years) were recruited for Experiment-1. Fifteen participants (7 females; mean age 22.6 ± 2.4 years) were included in the analyses (see *Quantification and statistical analysis* section). This was a within-subjects experiment design consisting of four ccPAS conditions and 5 timepoints. PR was assessed through the motion quartet task before (BSL), immediately (POST-0), 30 (POST-30), 60 (POST-60) and 90 (POST-90) minutes after each ccPAS session.

ccPAS was administered over the left and right V5/MT+ through two 40 mm figure-of-eight coils connected to two independent Magstim 200[2] stimulators (Magstim Company, Whitland, UK), delivering single monophasic waveform pulses. 90 pairs of pulses were delivered every 10 seconds (0.1 Hz) over a period of 15 min[7,22,26] at a fixed intensity of 70% of the maximum output stimulator[7] Coils were placed tangentially to the scalp with the handles pointing upwards and 45° laterally relative to the sagittal plane[7,21]. V5/MT+ sites were localized 3 cm dorsal and 5 cm lateral from the inion following the same procedures as in previous TMS studies[7,21,35,45–47]. These scalp locations have been indicated to correspond to the V5/MT+ sites by several studies using functional TMS localiser (i.e. via phosphenes induction)[45,48–52], including a previous study from our lab[21] in which the very same stimulators and coils as here were used. These locations are also consistent with the coordinates as indicated by neuroimaging localizers[11,35,53]. For each participant, 4 ccPAS configurations were tested. ccPAS sessions were delivered in pseudorandomized order, separated by at least 24 hours (mean 4.2 days; range 1-18). The design consisted of 2 experimental (lV5-rV5 and rV5-lV5) and 2 control (V5&V5_t0 and lV5-rV5_sham) ccPAS conditions. In 2 experimental conditions (lV5-rV5 and rV5-lV5) the interpulse interval (IPI) was 25 ms[2,23], i.e. the assumed mean conduction time of the targeted connection. In lV5-rV5, each pair of pulses was delivered first to lV5 and then to rV5. In rV5-lV5 the stimulation order was reversed. In the control condition V5-V5_t0, simultaneous pairing of pulses on lV5 and rV5 areas were delivered with an IPI of 0 ms. lV5-rV5 was administered also in lV5-rV5_sham with the TMS coils were tilted, so that no magnetic stimulation was effectively applied to the participant.

**Experiment-2**

Fifty-four participants (30 females; mean age 25.8 ± 6.1 years) were recruited for the behavioral Experiment-2. They were presented with the horizontal motion direction task to disclose preferential perception for rightward or leftward horizontal motion.

**Experiment-3**

In Experiment-3 a subsample of the 54 participants of Experiment-2 was selected. Seventeen subjects (11 females; mean age 22.6 ± 3 years) were recruited for Experiment-3 based on their performance (none of them showed a consistent rightward bias), availability and compatibility with brain stimulation procedures. To confirm the consistency of the leftward motion bias participants were asked to perform twice the horizontal motion direction task before (BSL-2, BSL-3) ccPAS administration, whilst the stimulation effect was tested immediately (POST-0) and 30 minutes (POST-30) after the end of ccPAS administration.

**QUANTIFICATION AND STATISTICAL ANALYSIS**

Performance on the motion quartet task (specifically MoCS task) was indexed by the PR value. The relationship between the behavioral records of vertical perception and the 8 aspects ratios (expressed as vertical distance, being the horizontal distance fixed) of the task was clearly sigmoidal: The larger the vertical distance the higher the records of vertical motion perception and vice versa. Thus, the logistic function (1) was fitted to these data.

(1) $\quad y = \dfrac{a}{1+e^{-\frac{x-b}{c}}}$

The inflection point (parameter *b*) of the estimated curve represents the vertical distance (as ° of visual angle) between the dots leading to equal horizontal and vertical motion perception, or the PR. Non-linear regression analyses to fit the logistic functions were computed with MATLAB (lsqcurvefit function, Levenberg-Marquardt algorithm).

In the horizontal motion direction task, rightward perception response was coded as 1 and leftward as -1. Thus, a value of 0 represented no bias, whilst negative and positive values indicated a leftward and a rightward preference, respectively.

Sample size of Experiment-1 was selected based on a previous ccPAS study of our laboratory[21], where 16 participants were tested. We tested 17 participants foreseeing a few dropouts, indeed 2 participants withdrew from the study after 2 and 3 of the 4 experimental sessions, therefore their datasets were excluded from the final analyses. In Experiment-3 we replicated the sample size of Experiment-1.

For Experiment-1, PR values were entered in a repeated measures factorial ANOVA with the within-subjects factors Stimulation (lV5-rV5, rV5-lV5; V5&V5_t0; lV5-rV5_sham) and Time (BSL, POST-0, POST-30, POST-60, POST-90). The resulting significant interaction was further explored in each ccPAS condition through four one-way ANOVAs with the factor Time. To directly test for differential lV5-rV5 and rV5-lV5 ccPAS effects (similarly, see also Table S2), an ANOVA was conducted with the within-subjects factors Stimulation (lV5-rV5, rV5-lV5) and Time (POST-0, POST-30, POST-60, POST-90). In Experiment-2 a one-sample two-tailed *t*-test against 0 was computed on the horizontal motion direction task scores to assess overall bias of the sample. In Experiment-3 a univariate repeated measures ANOVA with the within-subjects factor Time (BSL-2, BSL-3, POST-0, POST-30) was computed on the horizontal motion direction task scores.

Alpha value was set to 0.05. Where appropriate, post-hoc analyses were performed using <mark>Dunnett's test to compare post ccPAS measurements to the relative baseline value. To explore the interaction of the analysis directly testing the difference between lV5-rV5 and rV5-lV5 stimulations, planned *t*-test comparisons were performed on baseline corrected data.</mark> Effect size of significant ANOVA main effects/interactions are reported as partial eta squared ($\eta_p^2$), whilst Cohen's $d_{rm}$ and Cohen's $d_z$ indicate effect size for significant repeated-measure and one-sample *t*-tests, respectively, according to Lakens' guidelines[54]. By convention, $\eta_p^2$ of 0.01, 0.06, and 0.14 are and Cohen's *d* of 0.2, 0.5, and 0.8 are considered small, medium, and large effect sizes, respectively[55]. Statistical analyses were performed using Statistica (StatSoft Inc., Tulsa, OK). Throughout the text, means and relative ± standard deviations (SD) are reported, except for Experiment-2 and Experiment-3, where standard error of the mean (SE) is indicated as a dispersion index.

## ADDITIONAL RESOURCES

## KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---|---|---|
| **Deposited data** | | |
| Data for all experiments reported in this paper | This paper | Open Science Framework: https://osf.io/tc378/ |
| Demonstrative videos of the stimuli | This paper | Open Science Framework: https://osf.io/tc378/ |
| **Software and algorithms** | | |
| Statistica 12 | StatSoft Inc. | RRID: SCR_014213 |
| MATLAB v. 2012b | The MathWorks Inc. | RRID: SCR_001622 |
| Psychtoolbox 3 | psychtoolbox.org | RRID: SCR_002881 |
| E-prime Software | Psychology Software Tools, Inc. | RRID: SCR_009567 |
| **Other** | | |
| Magstim 200$^2$ Stimulator | Magstim Company | www.magstim.com |
| Magstim Rapid$^2$ Stimulator | Magstim Company | www.magstim.com |

**Lead contact**

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Vincenzo Romei: vincenzo.romei@unibo.it

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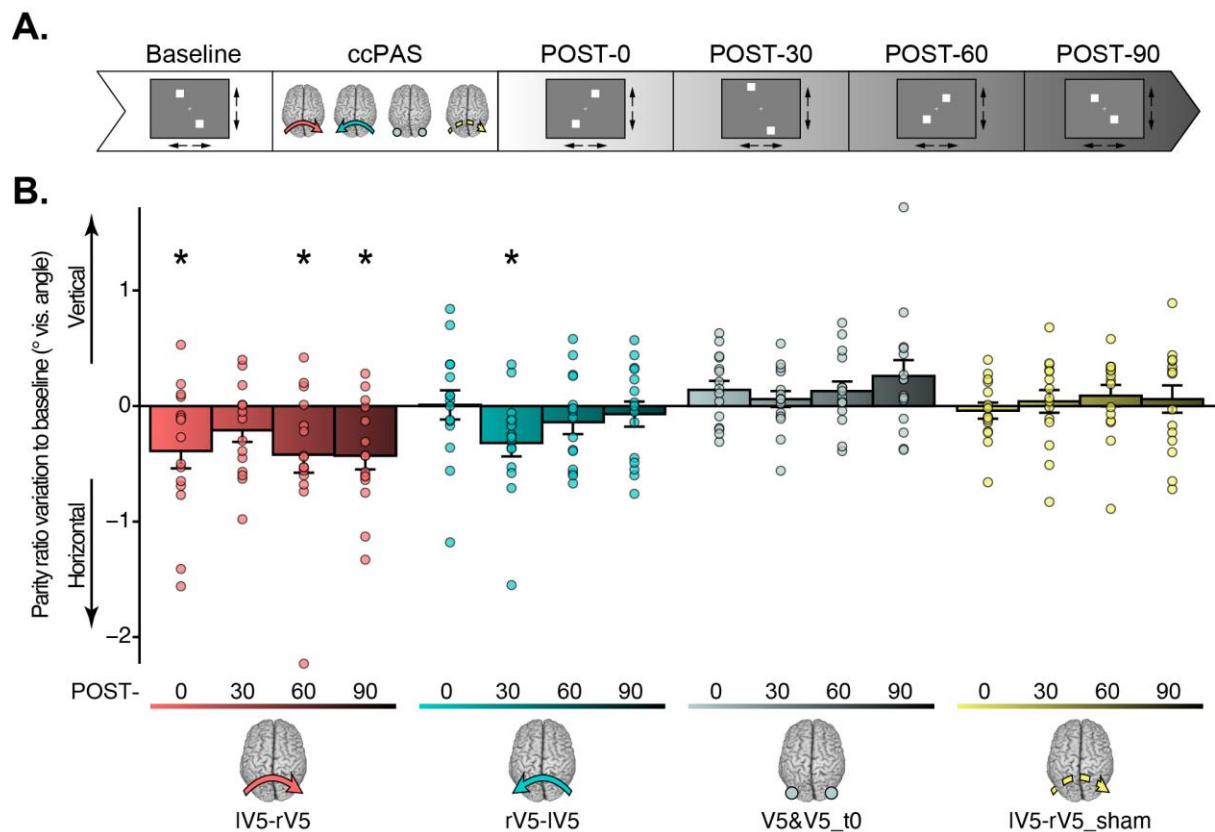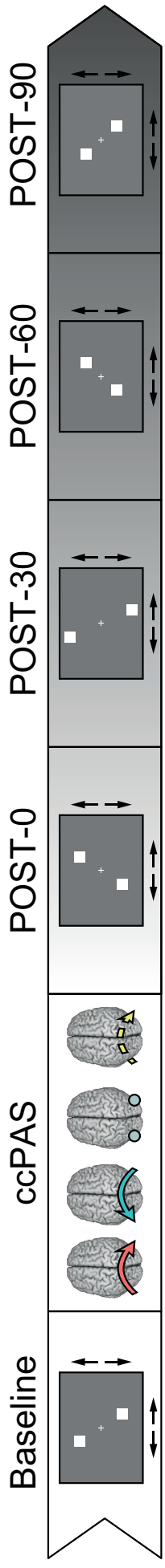
**Figure 1. Design and results of Experiment-1: interhemispheric V5 ccPAS enhances horizontal over vertical motion perception.** (A) Participant's parity ratio (PR) was assessed using the motion quartet task before and in four timepoints after ccPAS. This procedure was repeated over four different days in which all ccPAS conditions were delivered. (B) Compared to baseline, parity ratio decreases at 0, 60 and 90 minutes after lV5-rV5 ccPAS and 30 minutes after rV5-lV5 ccPAS, indicating enhancement of horizontal over vertical motion perception. No modulation of PR were observed in any other condition. Error bars indicate the s.e.m., asterisks indicate significant differences as compared to the relative baseline. See Figure S1 and Table S1.
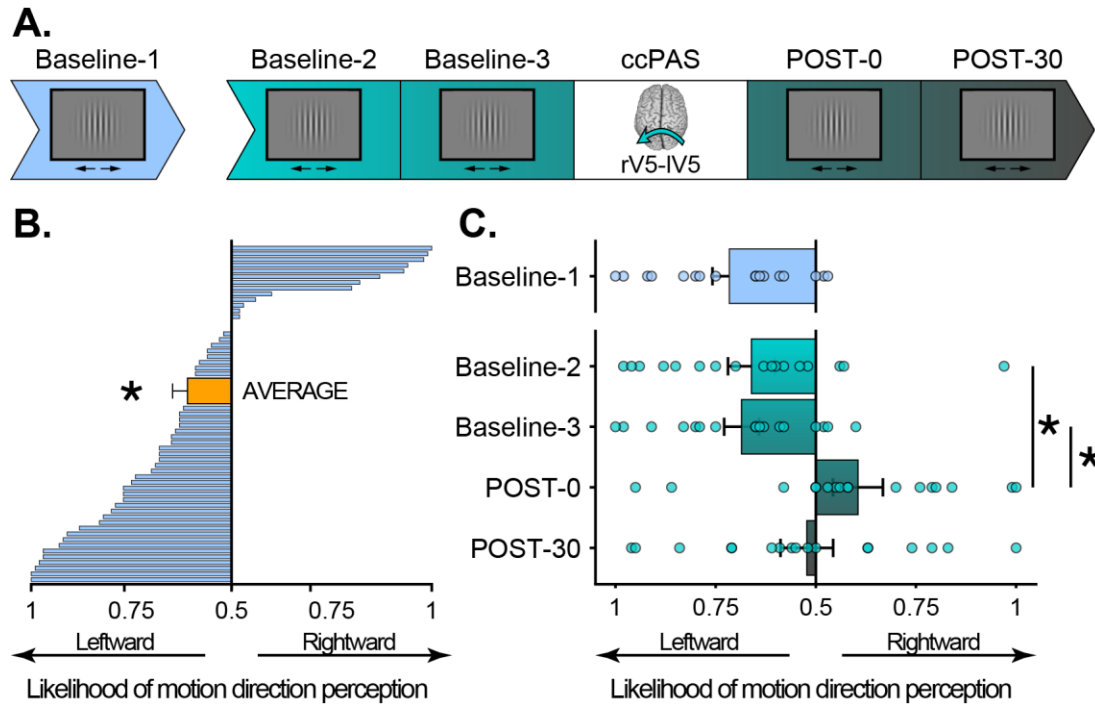
**Figure 2. Design and results of Experiment-2 and 3: right-to-left V5 ccPAS reverses the leftward horizontal motion perception preference.** (A) Participant's horizontal motion direction preference was assessed using the horizontal motion direction task in Experiment-2, as well as (on another day) two times before and two times after rV5-lV5 ccPAS, in Experiment-3. (B) The majority of the participants showed a preference to leftward motion perception, as depicted in the averaged score (orange bar). Each blue bar represents the performance of a participant. (C) Baseline-1, -2 and -3 demonstrate the stability of the perceptual bias which is reversed after ccPAS. Data in (B) and (C) are represented as the likelihood of motion direction perception. Error bars denote ± s.e.m., asterisks indicate significant comparisons. See Table S2.
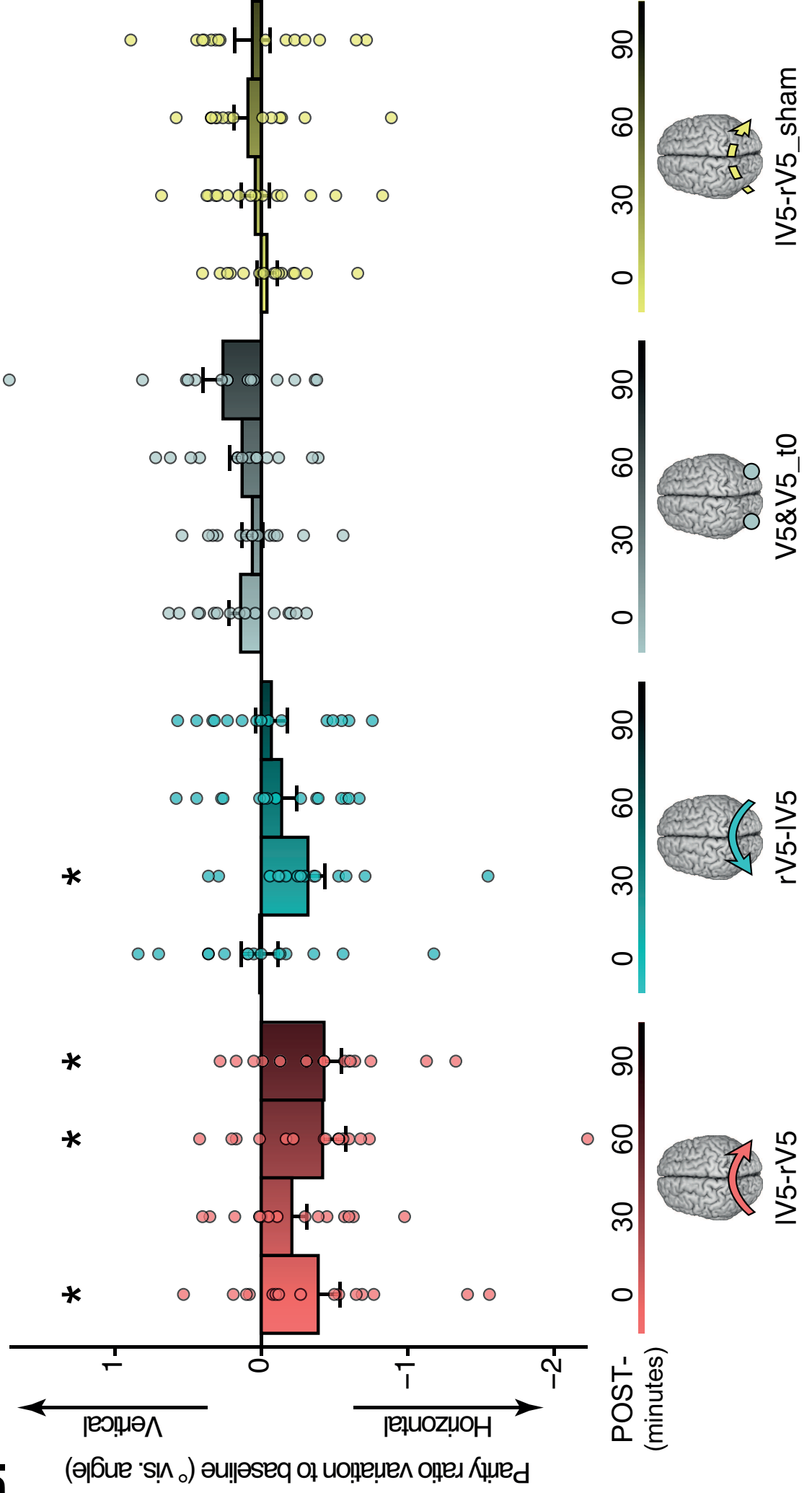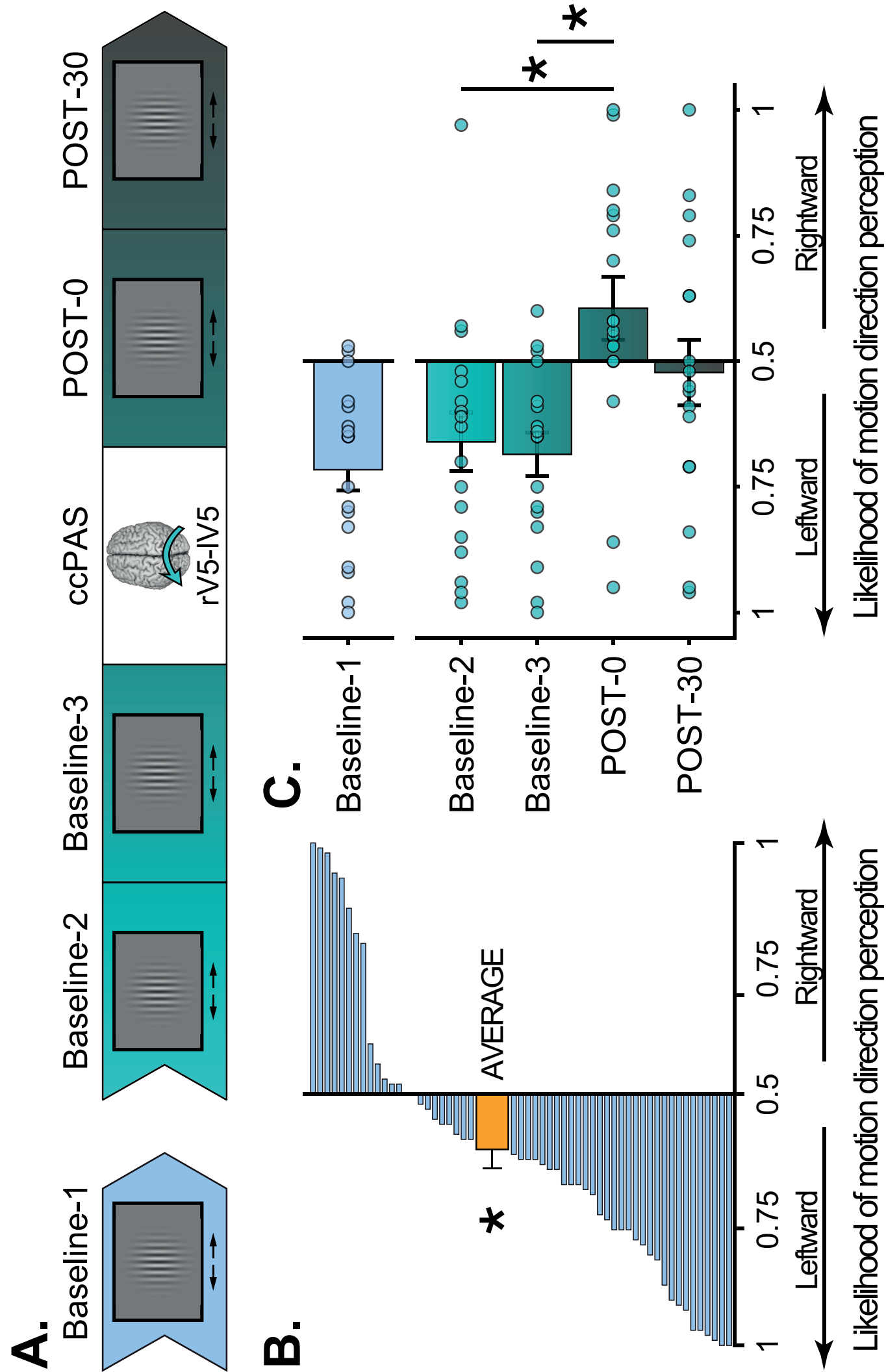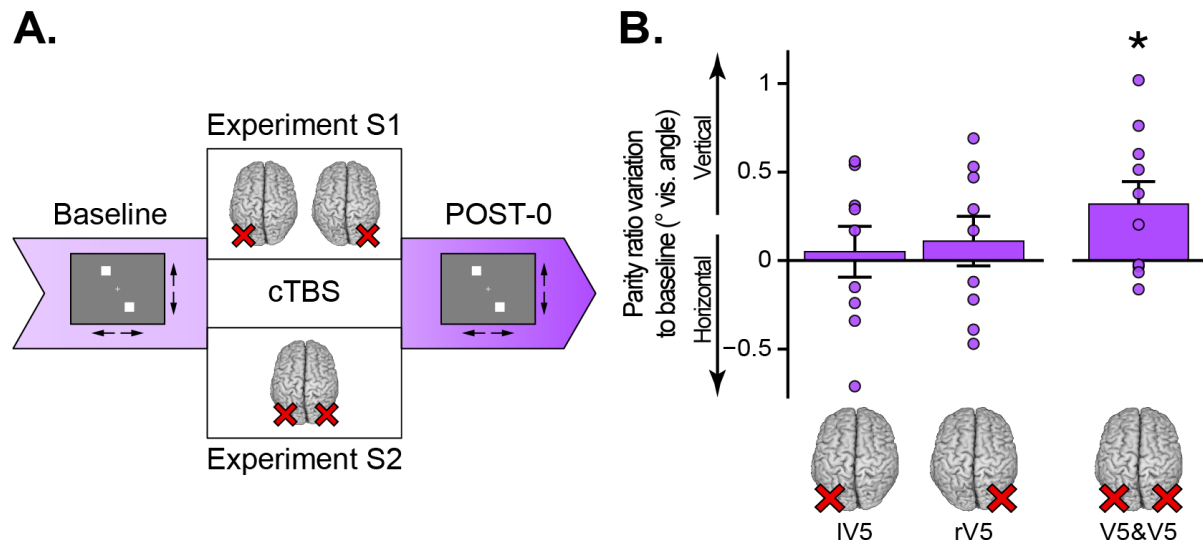
Figure 1

Figure 2

# Supplemental information

## Control Experiments

**A.**



**B.**



**Figure S1. Methods and results of Experiments-S1 and S2, related to Figure 1.** Experiment-S1 and S2 examined the extent to which the asymmetry found in the interhemispheric V5-V5 connections in Experiment-1 results from the potentiation of the lV5-rV5 pathway, or whether it may be linked to a distinctive functional role of the lV5 as opposed to rV5 in horizontal apparent motion. (A) We assessed the parity ratio (PR) values in two blocks following the procedure described for Experiment-1. Between the two blocks we applied continuous theta burst stimulation (cTBS) comprising three 50 Hz pulses at 5 Hz for 40 seconds delivered at 40% of the maximum stimulator output [S1] using a Magstim Rapid[2] biphasic stimulator (Magstim, Whitland, UK). In Experiment-S1, we delivered cTBS on lV5 or rV5 in 9 participants (4 females; mean age 22.9 ±2 years; three of them took part also in Experiment-2) over two separate sessions performed in different days (mean 3.5 days, range 1-4). In Experiment-S2 we delivered cTBS bilaterally over both rV5 and lV5 (only a few seconds apart) in 10 volunteers (5 females; mean age 25.8 ±7.3 years; one participated in Experiment-1, one in Experiment-2, two in Experiment-S1). (B) In Experiment-S1, the PR values collected before and after cTBS indicated no significant modulation (repeated measure ANOVA with factors Hemisphere (lV5, rV5) and Time (BSL, POST-0); all ps>0.38) demonstrating that increased horizontal motion sensitivity is not linked to a specialized role of the lV5 or rV5 on horizontal apparent motion but rather results from the potentiation of connectivity in the V5-V5 pathway. In Experiment-S2, bilateral V5 cTBS led to a significant increase of PR values (paired-sample two-tailed $t$-test; $t_9$=2.52, p=0.033, *Cohen's d*=0.3), suggestive of a reduced motion sensitivity for horizontal versus vertical apparent motion perception. This demonstrates that the ability to integrate local features from both hemifields during horizontal apparent motion rely on the involvement and communication of both V5 areas.

## Control Data

|  | BSL | POST-0 | POST-30 | POST-60 | POST-90 |
|---|---|---|---|---|---|
| **lV5-rV5** | 6.76 ± 0.14 | 6.37 ± 0.19 | 6.55 ± 0.16 | 6.33 ±0.24 | 6.33 ± 0.18 |
| **rV5-lV5** | 6.62 ± 0.14 | 6.63 ± 0.17 | 6.3 ± 0.18 | 6.48 ± 0.15 | 6.55 ± 0.15 |
| **V5&V5_t0** | 6.54 ± 0.14 | 6.5 ± 0.15 | 6.58 ± 0.17 | 6.63 ± 0.19 | 6.6 ± 0.14 |
| **lV5-rV5_sham** | 6.42 ± 0.13 | 6.57 ± 0.14 | 6.48 ± 0.16 | 6.55 ± 0.17 | 6.68 ± 0.21 |

**Table S1. Data of Experiment-1, related to Figure 1.** Non-transformed raw PR values measured on the bistable motion quartet in Experiment-1 along the five timepoints of assessment and across the four ccPAS conditions. Data are expressed in degrees of visual angle indicating the vertical separation between the dots of the bistable motion quartet. The mean ± s.d. are reported.

| Factor S | ANOVA effects | Planned comparisons |
|---|---|---|
| lV5-rV5, rV5-lV5 | S x T: $F_{3,42}$=3.21, p=0.032, $\eta_p^2$=0.19 | POST-0: p=0.044, *d*=0.75 <br> POST-90: p=0.029, *d*=0.83 |
| lV5-rV5, V5&V5_t0 | S: $F_{1,14}$=21.6, p<0.001, $\eta_p^2$=0.61 | |
| lV5-rV5, lV5-rV5_sham | S: $F_{1,14}$=15.5, p=0.001, $\eta_p^2$=0.53 | |
| rV5-lV5, V5&V5_t0 | S x T: $F_{3,42}$=3.29, p=0.03, $\eta_p^2$=0.19 | POST-30: p=0.005, *d*=0.85 |
| rV5-lV5, lV5-rV5_sham | T: $F_{3,42}$=3.93, p=0.015, $\eta_p^2$=0.22 <br> S: $F_{1,14}$=6.41, p=0.024, $\eta_p^2$=0.31 | |

==**Table S2. Supplemental analyses of Experiment-1.** Significant results of a series of ANOVAs with within-subjects factors Stimulation (S; 2 levels, see below) and Time (T; POST-0, POST-30, POST-60, POST-90) conducted on baseline corrected PR values. Relevant planned *t*-test comparisons were conducted for significant S x T interactions on baseline corrected PR values (see Figure 1B), effect size is indicated as *Cohen's d* (*d*). These analyses directly compare experimental (lV5-rV5, rV5-lV5), and experimental and control (V5&V5_t0, lV5-rV5_sham) conditions of stimulation. Significant main effects (or interactions) with the factor S, indicate that both experimental ccPAS differ from control ccPAS, as well as from each other.==

| BSL-1$_{Exp2}$ | BSL-2 | BSL-3 | POST-0 | POST-30 |
|---|---|---|---|---|
| -43.2 ± 8.4 | -32.1 ± 11.7 | -37.1 ± 8.7 | 21.1 ± 12.5 | -4.5 ± 13.1 |

**Table ==S3==. Data of Experiment-3, related to Figure 2.** Non-transformed raw scores of the participants of Experiment-3 on the horizontal motion task along the four timepoints of assessment. Note that BSL-1 refers to participants' score in Experiment-2. The mean ± s.e.m. are reported; negative and positive values indicate leftward and rightward motion perception, respectively (see STAR Methods for details).

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S1.    Huang, Y.Z., Edwards, M.J., Rounis, E., Bhatia, K.P., and Rothwell, J.C. (2005). Theta burst stimulation of the human motor cortex. Neuron *45*, 201–206.