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Neural Activity Reflecting Perceptual Awareness of Biologically Relevant Events*

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Humans are remarkably good at interpreting the identity and intentions of other people based on "body language" - dynamic cues portraying bodily movements. Befitting the important social significance of this perceptual ability, the human brain contains neural machinery uniquely responsive to the kinematics specifying human activity, including "biological motion" portrayed using just a small number of motion tokens specifying articulations of the body and limbs. We have established stimulus conditions that dissociate neural activity produced by presentation of biological events outside of conscious awareness from neural activity associated with conscious visual awareness of those events. We have used those stimulus conditions in concert with functional magnetic resonance imaging (fMRI) to measure neural responses in the posterior superior temporal sulcus (STSp), a crucial component in the neural network believed to underlie perception of biological motion. STSp was activated only when people actually perceived biological events and not when those events were registered outside of conscious awareness. These results provide direct evidence in support of the growing conviction that STSp, situated uniquely at the confluence of dorsal and ventral stream pathways, is intimately involved in actual perception of biologically relevant events.

Key words : biological motion, binocular rivalry, STSp, conscious visual awareness, fMRI

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Humans are remarkably good at interpreting the identity and intentions of other people based on “body language” - dynamic cues portraying bodily movements. This remarkable human ability is well illustrated by perception of biological motion, point-light animations depicting human activities by just a small number of motion tokens specifying articulations of the body and limbs (Ahlström, Blake, & Ahlström, 1997; Johansson, 1973). Upon viewing these simple kinematics, most people readily recognize not only the activities but the gender and emotion of the person portrayed by dots from motion information alone (Dittrich, Troscianko, Lea, & Morgan, 1996; Kozlowski & Cutting, 1977; Mather & Murdoch, 1994; Troje, 2002). The ability to recognize bodily movements also develops very early in age, which is evidenced by the finding that point-light biological motion animation is sufficient for reliable recognition at an age of 3 years (Pavlova, Krägeloh-Mann, Sokolov, & Berbaumer, 2001).

Befitting the social significance of this perceptual ability, the human brain contains neural machinery uniquely responsive to kinematics. Especially, a cortical region on the posterior superior temporal sulcus (STSp) is well-known as a crucial component in the neural network believed to underlie perception of biological motion (Allison, Puce, & McCarthy, 2000; Bonda, Petrides, Ostry, & Evans, 1996; Grossman, Blake, & Kim, 2004; Grossman, Donnelly, Price, Pickens, Morgan, Neighbor, & Blake, 2000; Kim, 2012; Pyles, Garcia, Hoffman, & Grossman, 2007; Servos, Osu, Santi, & Kawato, 2002).

The specific role of the STSp in biological motion perception, however, has not yet been fully elucidated. Several studies have suggested that the BOLD signal within this region is modulated by observers' understanding of human movement and, therefore, task-dependent (Pavlova, Sokolov, Birbaumer, & Krägeloh-Mann, 2008; Pelphrey & Morris, 2006; Wyk, Hudac, Carter, Sobel, & Pelphrey, 2009). For example, Wyk et al. (2009) showed an enhanced activity of right STSp when observers perceive another person's motion congruent with his/her intentions. Nonetheless, the specific relationship between STSp and perceptual awareness of an observer remains unanswered. In other words, it is not certain that what activates this area is either presentation of socially meaningful stimuli or observer’s conscious perception of them.

A potential answer to this question was suggested by a recent fMRI study showing indistinguishable STSp activation associated with observers' incorrect recognition of non-biological motion as biological from that associated with observers' correct recognition of biological motion as biological (Kim, Park, & Blake, 2011).

Therefore, Kim et al. (2011) implied that STSp reflects observers' recognition of biological motion, not just physical presence of it. However, it is still uncertain whether biological motion outside conscious awareness can still elicit increase in activation in the STSp or it should be accompanied by conscious awareness to elicit increase in activation in the STSp.

To answer this question, we sought to establish stimulus conditions that dissociate neural activity produced by presentation of biological events from neural activity associated with conscious visual awareness of those events. Binocular rivalry - alternations in visual awareness between conflicting visual stimuli presented to corresponding areas of the two eyes (Blake & Logothetis, 2002) - provides a paradigmatic phenomenon for manipulating visual awareness (Crick, 1996; Kim & Blake, 2005). In exploiting the phenomenon of binocular rivalry, we adapted a probe technique for a more robust and objective psychophysical procedure, proven to be fairly effective in testing observers ' mental states of "visual unawareness" induced during suppression phases of binocular rivalry (Blake, Yu, Fukuda, & Lokey, 1998). Previous studies on binocular suppression suggest that changes of suppressed stimuli, if not abrupt, cannot be detected for several seconds. For example, observers fail to detect changes in the spatial frequency or the orientation of a suppressed grating (Blake & Fox, 1974) or transitions from incoherent motion to coherent motion (Blake et al., 1998). In the current work, point-light animations portraying different human activities were presented as probes during dominance phases and during suppression phases of rivalry while observers experienced perceptual alternation between two rival targets.

Before utilizing this experimental procedure in concert with functional magnetic resonance imaging (fMRI), we examined carefully the effectiveness of the method. This was necessary because probes in most of the previous studies were arguably simple and uninformative, whereas the probes we used in this experiment - biological motion animations - are highly interesting to observers and bear social significance. Therefore, it was probable that this special sort of visual stimuli might penetrate "perceptual unawareness" during rivalry suppression and be detected more easily (Alpers & Pauli, 2006; Anderson, Siegel, Bliss-Moreau, & Feldman Barrett, 2011; Yoon, Joormann, Hong, & Kang, 2009). Biological motion animations, indeed, have been shown to behave differently from other simple and uninformative stimuli during binocular rivalry. For example, recognizable biological motion as a rival target showed decreased suppression and faster alternation than less recognizable motion stimuli (Beintema, Halfwerk, & van Wezel, 2004). With

these doubts in mind, we needed to question if these biologically important changes go undetected during suppression phases of binocular rivalry. We would then be able to ask whether biological events presented during suppression phases of rivalry - and, hence, outside of visual awareness - are nonetheless registered by STSp. Reported below are the results from this experiment.

Methods

Observers Five individuals (3 male, 2 female) participated in this experiment. All participants had normal or corrected to normal vision, and had no history of neurological disorders. Prior to participation the observers gave informed, written consent. The protocol was approved by the Vanderbilt Institutional Review Board.

Stimuli Stimuli were presented on a 21-inch NEC monitor (1024 x 768 resolution, 60 Hz frame rate) under the control of a Macintosh computer. A pair of rival targets was viewed dichoptically. One of the rival targets was a radial grating which counterphase-flickered at 20 Hz and the other was an array of 12 gaussian-filtered dots moving randomly within a virtual window (see Figure 1a). Rival targets subtended 1.1 x 1.7 degree of visual angle, and were surrounded by a square black and white checker border to promote stable binocular alignment.

For probes, we created point-light animations portraying a person engaged in 25 different activities, including walking, running, kicking and throwing. Activities of the person wearing dark clothing and attaching light bulbs on his major joints were videotaped and digitized. 12 dots (each subtending approximately 10 arc min of visual angle) replaced light bulbs and the initial positions and motion vectors of the dots were encoded. Scrambled animations were also created by rearranging the initial dot positions of each biological animation. Thereby, scrambled animations retain the same motion vectors as in biological motion animations, but the biologically important information was destroyed (see Figure 1b).

Psychophysics outside the fMRI scanner. Each observer completed 5 blocks for each of the two rivalry conditions: dominance condition and suppression condition. Blocks were run in two separate sessions in terms of the rivalry condition, with the order of these two sessions counterbalanced for each observer. Each block consisted of 16 trials and each rival target was presented an equal number of times to the left and right eyes. Dichoptic presentation was established by using a mirror stereoscope. In the

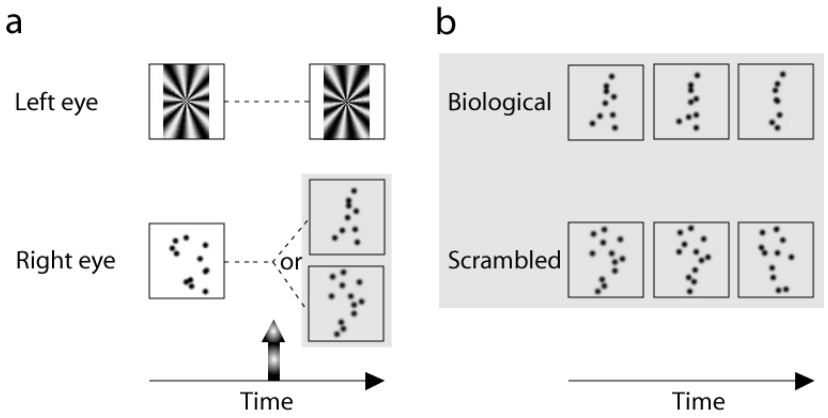

Figure 1. Experimental design and stimuli. a. Schematic of experimental procedure. One eye viewed a flickering radial grating and the other eye viewed 12 dots moving randomly within a virtual window identical in size to the radial grating. The observer tracked fluctuations in rivalry dominance, and at irregular times (arrow) random dots briefly dissolved smoothly into biological motion or into scrambled motion. Transitions could occur at the onset of dominance or at the onset of suppression, and following each transition both displays disappeared and the observer indicated which kind of sequence had been presented. b. Detailed schematic of probes corresponding the shaded part of a.: biological (top) and scrambled (bottom) motion sequences.

dominance condition, the observer pressed a switch when the radial grating was completely suppressed and only the randomly moving dots were seen. This triggered a brief (45 frames: 750 ms), smooth transition of dots from random motion to point-light biological animation or scrambled versions of each animation. At the end of the 750 ms period both rival targets disappeared. Following each transition, the observer made a 2 alternative forced choice judgment, guessing if necessary, by pressing one of two buttons to indicate if biological motion animation was presented. In the suppression condition, the observer pressed a switch when the randomly moving dots were completely suppressed and the radial grating was perceived in its entirety.

MRI Acquisition Brain imaging was performed on a 3T GE Signa MR scanner located within Vanderbilt University Medical School. High-resolution T1 anatomical images were collected for each of the five observers (184 slices, 1.0 x 1.0 x .9375 mm). Functional images were collected using 9 axial oblique slices selected to cover the occipital, posterior parietal, and ventral temporal cortices (slice thickness 5 mm with no gap, in-plane resolution 3.75 x

3.75 mm). Gradient-recalled echoplanar imaging was used to localize STSp and MT+ (TR = 2000 ms, TE = 30 ms, flip angle = 70) and for rivalry, stimulus alternation, and the baseline control scans (TR = 1000 ms, TE = 30 ms, flip angle = 70).

Localizer Scans. Stimulus displays were viewed on MR-compatible LCD monitors mounted inside goggles (Resonance Technology, Inc.). Each of the two STSp localizer scans lasted 4 min, the initial 8 sec (4 volumes) of which were discarded prior to analysis to allow for MR stabilization. The 4-min scan was divided into 7 blocks of biological and 7 blocks of scrambled motion. Within each 14-sec block, seven 1 sec animations were presented with an inter-stimulus interval of 1 sec. A fixation cross remained visible throughout the scan, and the observer was instructed to maintain fixation while attending to the entire stimulus. The observer was engaged in a 1-back task to promote attention. The observer indicated with a button press whenever animation was the same as the previous. Following two STSp localizer scans, two MT+ localizer scans were performed. An MT+ localizer scan lasted 4 min 16 sec, the initial 8 sec (4 volumes) of which were discarded prior to analysis to allow for MR stabilization. The 4 min 16 sec scan was divided into 8 blocks of moving dots and 8 blocks of static dots. The motion stimulus was an optic flow of 500 dots moving within a circular aperture and the static stimulus was a snap-shot of the motion stimulus. The observer was instructed to fixate on the center of the aperture throughout the scan.

Binocular Rivalry Scans. Rival targets were dichoptically presented on MR-compatible LCD monitors mounted inside goggles. For four of the five observers, each rival target was presented an equal number of times to the left and right eyes in separate runs. For one observer (O2), moving dots were almost always presented to the left eye due to the severe right eye dominance. The observer viewed the pair of rival targets while tracking his/her perceptual alternation by pressing one of two buttons for at least 14 sec. After some period of rivalry tracking, dots were briefly (45 frames: 750ms), coalesced into one of 25 point-light biological motion animation followed by the observer's pressing one of two buttons (About a half of the total binocular rivalry scans also included scrambled motion animation.). Each run lasted 2min 24sec - 2min 34sec based on the observer's alternation speed. Within a run, about 4 biological motion probes were presented for each of the two rivalry conditions: dominance condition and suppression condition (For those runs including scrambled motion probes, about 2

biological motion and 2 scrambled motion probes were presented for each of the two rivalry conditions.). In the dominance condition, a probe (event) was introduced when the observer pressed the dot motion button indicating his/her exclusive perception of dot motion. In the suppression condition, a probe was introduced when the observer pressed the radial grating button indicating his/her exclusive perception of the radial grating (i.e. complete suppression of dot motion). At the end of the 750-ms period, dots depicting biological motion briefly changed back to random motion. The observer tracked his/her rivalry alternation for another 14sec until the next event happened. The order of two (or four) event conditions was randomly intermixed within a run.

Stimulus Alternation & Baseline Control Scans. For one of the five observers (O1) stimulus alternation scans were performed. These scans were identical to rivalry scans except that the stimulus alternated between monocular presentations of two rival targets. The temporal sequences reported by the same observer in the previous rivalry scans were used to alternate two rival targets. For the dominance condition, biological animation probes were briefly introduced and faded back to random motion. For the suppression conditions, biological animation probes were not shown and only the radial grating remained to be seen to mimic real rivalry scans. For the same observer, baseline control scans were also performed. These scans were identical to the stimulus alternation scans except that biological motion probes were also shown to replace the radial grating (suppression condition) as well as the random motion (dominance condition).

Functional MRI Data Analysis. Image preprocessing was conducted in Brain Voyager 4.5 (Brain Innovations, Inc.). All images were detrended to remove any linear drift in time, multifiltered with a 4-mm FWHM spatial filter, and motion corrected.

Localizer scans. For each observer, STSp was localized using the subtraction method. The STSp ROIs were created from voxels highly correlated ($p < .001$) with viewing biological versus scrambled motion in the averaged localizer scans. MT+ was also localized using the subtraction method. The MT+ ROIs were created from voxels highly correlated ($p < .00001$) with viewing moving versus static dots in the averaged localizer scans.

Rivalry and stimulus alternation scans. Raw MR signal of each run in the voxels defined as ROIs was averaged. The time series from 2 sec after each event onset to 15 sec

thereafter was extracted and divided by the intensity at the event onset to convert the data to units of fractional signal change. Signals were averaged following each introduction of probe event during dominance and, separately, following each introduction of probe event during suppression.

Results

Psychophysics outside the fMRI scanner Figure 2 shows percent-correct performance for the two rivalry conditions obtained from the 5 observers (this being a two-alternative forced-choice task, chance performance is 50 %). Results from the group analysis showed statistically significant difference in observers' recognition performance during dominance and during suppression ($t(4)=5.208$, $p<.01$, paired t-test, see Figure 2a). Specifically, observers were highly accurate distinguishing biological from scrambled motion in the dominance condition (94 ± 4%), whereas they performed poorly in the suppression condition (58 ± 6 %). Individual data showed the same pattern of results (Figure 2b); In the dominance condition, all 5 observers were highly accurate distinguishing biological from scrambled motion: O1, 99% correct; O2, 100% correct; O3, 78% correct; O4, 98% correct; O5, 95% correct). However, observers performed poorly in the suppression condition, with some scores being close to chance levels: O1, 64% correct; O2 69% correct; O3, 58% correct, O4, 46%

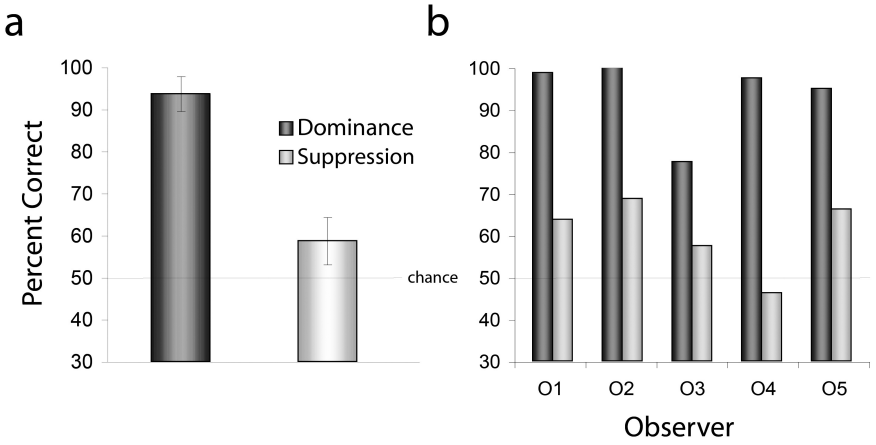

Figure 2. Percent-correct recognition (2 AFC task distinguishing biological from scrambled motion, chance level = 50%) for transitions during dominance and suppression. a. Group average from three observers. b. Individual results from each of the five observers (16 trials/condition within a block and 5 blocks for each condition resulting in 80 trials/condition as a total).

correct; O5, 59% correct). These results confirmed that normally visible biological motion probes often were difficult to perceive when presented during suppression phases. Earlier results had shown that people are essentially "blind" to changes in simple visual features (e.g., gratings) presented to a suppressed eye (Blake et al, 1998). The current results extend those findings and suggest that even interesting, socially relevant changes have little impact on visual awareness during suppression phases of binocular rivalry.

To test whether eye dominance affects awareness of the probes, we also analyzed percent-correct performance discriminating biological from scrambled motion presented to each of the two eyes separately for all five observers. Results showed that observers were highly accurate distinguishing biological from scrambled motion in the dominance condition regardless of the eye to which the probes were introduced: O1, 98% correct for the right eye probes, 100% correct for the left eye probes; O2, 100% correct for the right eye probes, 100% correct for the left eye probes; O3, 63% correct for the right eye probes, 88% correct for the left eye probes; O4, 95% correct for the right eye probes, 100% correct for the left eye probes; O5, 90% correct for the right eye probes, 100% correct for the left eye probes. Performance was also comparable between the eyes in the suppression condition for most observers as well: O1, 60% correct for the right eye probes, 68% correct for the left eye probes; O3, 50% correct for the right eye probes, 65% correct for the left eye probes; O4, 48% correct for the right eye probes, 45% correct for the left eye probes; O5, 70% correct for the right eye probes, 63% correct for the left eye probes. Only one observer O2 showed a large difference in recognition performance based on the eye condition: 90% correct for the right eye probes and 48% correct for the left eye probes. O2's relatively high recognition performance in the suppression condition may be attributable to severe right eye dominance, which might have played a role breaking suppression more often when biological motion events were introduced to the dominant eye. This became the basis for our decision to present moving dots always to the left eye (so that the probes were always introduced to the non-dominant eye) for O2 inside the scanner.

fMRI Biological motion sensitive area STSp was localized unilaterally (O1: right, O3: left, O5: right) or bilaterally (O2 and O4) in all five observers. Motion-sensitive area MT+ was also localized. One observer's localization results are shown in Figure 3. BOLD response during binocular rivalry scans were extracted from these functionally defined ROIs of each observer, and

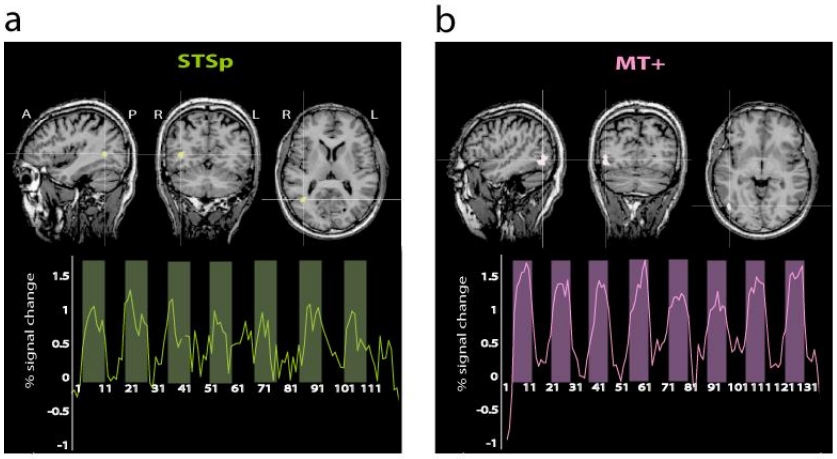

Figure 3. ROIs in an example observer. a. Top: Sagittal, coronal, and axial views of the STSp in the right hemisphere of O1. Bottom: BOLD activity plot is the average time course from the right STSp ROI of this observer during the biological and scrambled motion localizer. Light green bars indicate intervals of biological motion (order of blocks was counterbalanced across observers). b. Top: Sagittal, coronal, and axial views of the MT+ in the right hemisphere of O1. Bottom: BOLD activity plot shows the average time course from the right MT+ during motion and static dot localizer. Light purple bars indicate intervals of moving dots (order of blocks was counterbalanced across observers).

averaged separately for biological events introduced during dominance and for biological events introduced during suppression. Averaged time course of STSp activity for one observer and histograms of the averaged peak percent signal change (3-9 sec after event onset) for all five observers are shown in Figure 4a.

Results showed that biological motion sequences presented during dominance yielded reliable BOLD signals, but the same sequences presented during suppression yielded weak BOLD signals indistinguishable from baseline levels within STSp of all five observers. Differences in BOLD signal between conditions are highly significant in most of the five observers (O1: $t(51)=7.162$, $p<.001$, O2: $t(62)=2.458$, $p<.05$, O3: $t(53)=1.936$, $p<.05$, O4: $t(25)=1.629$, n.s., O5: $t(31)=2.143$, $p<.05$; paired t-test). Also within right MT+ of all five observers, biological motion sequences presented during dominance yielded reliable BOLD signals, but the same sequences presented during suppression yielded weak BOLD signals indistinguishable from baseline levels (O1: $t(51)=3.573$, $p<.001$, O2: $t(62)=1.784$, $p=.07$ (marginally significant), O3: $t(53)=2.689$, $p<.01$, O4: $t(25)=.892$, n.s.,

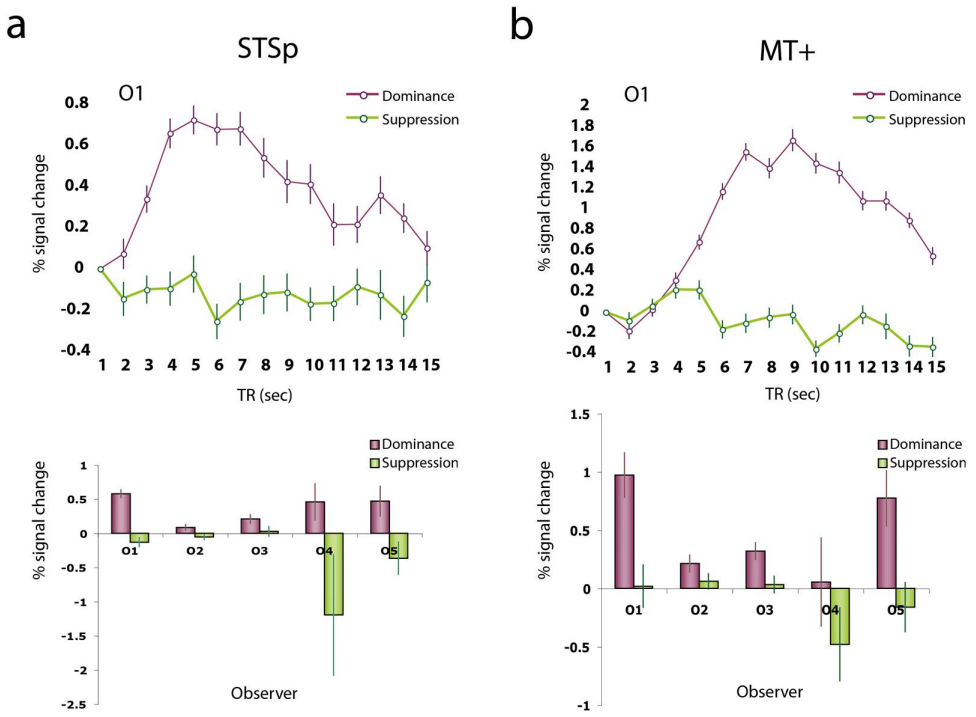

Figure 4. a. Top: Averaged time course of STSp in the dominance (purple) and the suppression (green) conditions for O1. Error bars denote ± 1 standard error of the mean. Bottom: The averaged peak percent signal change (3-9 sec after event onset) for in the STSp of all five observers. b. Top: Averaged time course of MT+ in the dominance and the suppression conditions for O1. Error bars denote ± 1 standard error of the mean. Bottom: The averaged peak percent signal change (3-9 sec after event onset) for in the MT+ of all five observers.

O5: $t(29)=2.648$, $p<.05$; paired t-test).

In the initial, approximately a half of the total number of event-related scans, we also included trials on which the random-motion rival target sometimes was replaced by sequences depicting scrambled motion. Scrambled motion animations failed to yield BOLD activation even during dominance within STSp, confirming that the responsiveness of this area during dominance was indeed selective for transitions from random to biological motion. By contrast, scrambled motion animations did yield BOLD activation during dominance within MT+. This finding reassured us that this area, unlike STSp, is not selectively responsive to biological motion but involved in processing of motion information in general (see Figure 5).

We also measured BOLD signals under

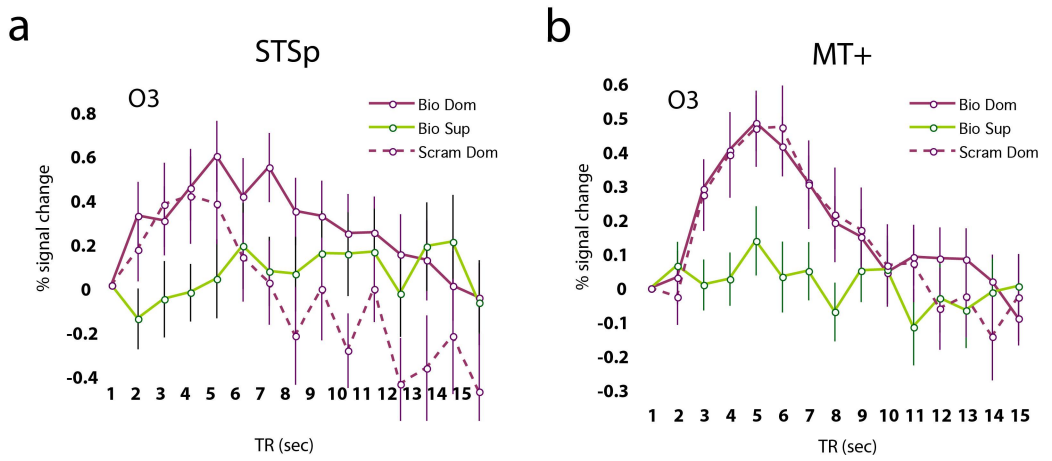

Figure 5. Results reassuring the differential functional roles STSp and MT+ play. a. Averaged time course of STSp in response to biological motion introduced to a dominant eye (purple solid) and to a suppressed eye (green solid) for O3. Averaged time course of the same region in response to scrambled motion introduced to a dominant eye (purple dashed) was added, which shows differential response of STSp to biological vs. scrambled motion ($t(28)=1.984$, $p<.05$; paired t-test). Error bars denote ± 1 standard error of the mean. b. Averaged time course of MT+ in response to biological motion introduced to a dominant eye (purple solid) and to a suppressed eye (green solid) for O3. Averaged time course of MT+ in response to scrambled motion introduced to a dominant eye (purple dashed) was added, which shows MT+'s comparable response to both biological and scrambled motion ($t(28)=.517$, n.s.).

several other conditions. To mimic the alternations of rivalry, the radial grating viewed by one eye and the random-motion pattern viewed by the other eye were alternately presented over time, following a time-course that mirrored the phenomenal alternations in dominance measured during rivalry. At irregular times during these alternating presentations, the random-dot pattern was briefly replaced by a biological motion sequence, mimicking what observers actually experienced during rivalry. BOLD signals to these brief, non-rival presentations were equivalent in magnitude to those measured during dominance phases of rivalry (Figure 6a), indicating that activations during dominance phases are equivalent to those associated with normal, non-rival viewing.

Another condition tested the possibility that BOLD signals in response to biological motion were reduced during suppression because observers had been seeing random motion for several seconds prior to the presentation of biological motion; in contrast, biological motion probes presented during dominance phases were

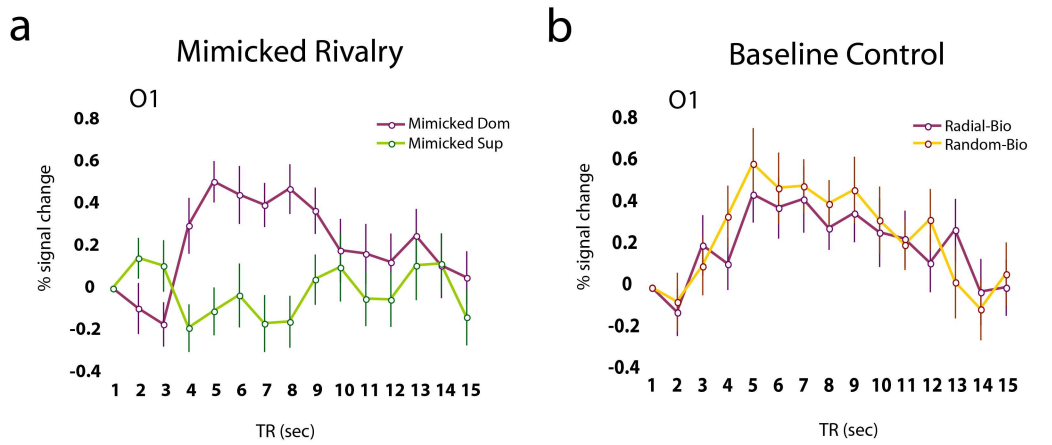

Figure 6. a. Rivalry mimic condition. Averaged time course of STSp activity for transitions from random to biological motion (mimicking dominance) and trials where the radial grating remained visible after 'event' onset (mimicking suppression). b. Baseline control condition. Averaged time course of STSp activity for brief transitions from random-dot motion to biological motion and from radial grating to biological motion.

preceded by several seconds of radial grating visibility. To determine whether the previously dominant stimulus, not the conscious awareness of the biological motion probes, was responsible for these differences in BOLD signal, we alternately presented the radial grating to one eye and the random-motion display to the other eye, again following a time-course that mimicked rivalry. At irregular intervals, either the grating or the dots were briefly replaced by a biological motion sequence, and the BOLD signals to this brief replacement were measured. Thus in one condition, biological motion was preceded by perception of the radial grating and in the other condition biological motion was preceded by perception of random-motion. Introduction of biological motion under both conditions yielded equivalent BOLD responses (Figure 6b), confirming that the reduction in BOLD signal amplitude to biological motion presented during suppression phases of rivalry (Figure 4) was not attributable to the nature of the visible stimulus preceding those presentations.

Discussion

Results from the current study showed that during binocular rivalry suppression, even socially meaningful visual information such as biological motion can go undetected. It was also shown that such undetected, invisible information leaves little signatures in STSp, a brain area selectively

responsive to visual events with social significance. These results allow us to draw a stronger conclusion about the functional role of STSp than did previous brain imaging studies.

We do not wish to imply that STSp alone mediates perception of biological motion, for other brain areas in both dorsal and ventral pathways are also selectively responsive to socially relevant visual events (Grossman & Blake, 2002; Grossman, Blake, & Kim, 2004; Ptito, Faubert, Gjedde, & Kupers, 2003; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001), including areas where activity is modulated during binocular rivalry (Tong et al., 1998) and areas where the emotional expressiveness of biological stimuli is important (Winston et al., 2002). In a future work it might be useful to examine the BOLD responses in other relevant regions, which was not entirely possible in the current work because of our slice positioning covering the whole occipital and the temporal lobes but leaving the dorsal part of the brain uncovered. Nonetheless, STSp may well be a crucial site of convergence of these distributed visual areas (Adolphs, 2003; Vaina et al., 2001), a lynchpin in the neural circuitry supporting social cognition including perception of biological motion (Adolphs, 1999; Allison et al., 2000; Blakemore & Decety, 2001; Brothers, 1990). Modulation of activity in STSp coincident with visual awareness confirms its intimate involvement in actual perception of biologically relevant visual events.

Of particular relevance to such results from the current work is a recent fMRI study showing strong STSp activation associated with non-biological motion when observers recognized it as biological (Kim, Park, & Blake, 2011). Specifically, Kim and colleagues presented biological and scrambled motion stimuli and monitored activation in the STSp region while observers made a detection judgement whether the given stimulus was biological. Observers' behavioral responses and associated neural responses were classified into signal detection categories including hit, correct rejection, and false alarm. Interestingly, STSp activity on false alarm trials was indistinguishable from that on hit trials, which suggests that STSp reflects observers' recognition of biological motion. Therefore, both Kim et al. (2011) and the current findings commonly show that STSp is involved in observers' experience of biological m otion, not just physical presence of it.

However, the current study can be differentiated from Kim et al. (2011) in terms of how the “experience of biological motion” was introduced. In the study by Kim and colleagues, the event (either biological or scrambled) was always visible and what was manipulated was observers' decision about the visible event. In contrast, we manipulated the visibility of the event (either

biological or scrambled) during binocular rivalry and confirmed that it was invisible when presented to the suppressed eye. Thus, the strong activation in the STSp associated with the false alarm trials in the previous study, as the authors wrote in the discussion section, might "result from top-down influences on perception of biological motion" (Thompson et al., 2005; Thornton, Rensink, & Shiffrar, 2002), whereas the stronger activation in the STSp during dominance than during suppression in the current work is related to conscious awareness of biological motion.

Concerning the "visibility" manipulation, one might question the effectiveness of the probe technique employed in the fMRI experiment where observers' conscious awareness was not examined on-line, unlike in psychophysics outside the scanner. However, BOLD responses within STSp and MT+ in the suppression condition indistinguishable from the baseline activity (Figure 4 & 5) suggest that the probe introduced to the suppressed eye was indeed largely "invisible". This was also evidenced by the results from the control experiment showing that the differential BOLD responses in the STSp to biological motion presented during the dominance and the suppression conditions were comparable to those actually presented and not presented (stimulus alternation scan, see Figure 6a). Therefore, the given STSp results seem to stem from the visibility of the probe introduced during dominance and suppression phases of binocular rivalry, not from other causes (baseline control scan, see Figure 6b), ensuring that STSp is modulated by conscious awareness of biologically relevant motion information, not mere existence of it.

One might also question the novelty of the current work, since neural activity reflecting visual awareness during binocular rivalry has already been shown in a number of studies. However, it should be noted that we are not merely determining whether neural activity is modulated when viewing rival targets, a tactic taken by several other fMRI investigations of binocular rivalry (Lumer, Friston, & Rees, 1998; Tong, Nakayama, Vaughan, & Kanwisher, 1998; Polonsky, Blake, Braun, & Heeger, 2000; Wunderlich, Schneider, & Kastner, 2005). In these previous studies, observers tracked spontaneous perceptual alternation between two dissimilar visual stimuli presented to the two eyes, and brain activity reflecting observer's conscious visual awareness was monitored. Instead, we have introduced conspicuous biological events during dominance phases and during suppression phases of binocular rivalry, to learn whether registration of those events transpires in the absence of conscious awareness. This event-related, probe procedure represents a novel, potentially revealing strategy which can

generate outcome that cannot be predicted based on earlier brain imaging results.

On a final note, our results can also be discussed in a more general context of neural responses to unconsciously processed stimuli, not just in terms of the specific role of the STSp region. Previous studies have shown that some biologically meaningful visual stimuli, even when registered outside of conscious awareness, elicit activation in the relevant brain regions. For example, brain imaging studies found activation in the amygdala without conscious access to the emotional stimuli such as affective faces (Morris, Frith, Perrett, Rowland, Young, Calder, & Dolan, 1998; Whalen, Rauch, Etcoff, Mclnerney, Lee, & Jenike 1998), some of which exploited binocular rivalry paradigm (Pasley, Mayes, & Schultz, 2004; Williams, Morris, McGlone, Abbott, & Mattingley, 2004). However, little has been known about brain responses to other classes of visual stimuli bearing social significance such as biological motion. Thus, the current finding - STSp, an area situated uniquely at the confluence of dorsal and ventral visual pathways (Blake & Shiffrar, 2007), showed little response to "invisible" biological motion stimuli - implies that the conclusion drawn from the previous studies cannot be generalized into other brain regions and other classes of stimuli.

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생물형 운동에 대한 시의식을 반영하는 신경 활동

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인간은 '신체 언어' -신체의 움직임을 표현하는 동적 정보-를 활용하여 다른 사람을 식별하거나, 다른 사람이 지닌 의도를 해석하는데 특별한 능력을 보인다. 이와 같은 지각 능력이 지닌 사회적 중요성을 반영하듯, 인간의 두뇌는 인간의 활동을 나타내는 운동 정보에 선택적으로 반응하는 신경 기제를 지니고 있다. 이러한 정보에는 제한된 수의 점을 활용하여 몸과 사지의 움직임을 나타내는 '생물형 운동'이 포함된다. 본 연구에서는 생물적 중요성을 지니는 사건의 제시가 의식적 자각을 동반할 때와 동반하지 않을 때에 각각 관여하는 신경 활동을 구별할 수 있는 자극 제시 조건을 설계하였다. 이러한 자극 조건과 함께 기능적 자기 공명 영상을 활용하여, 생물형 운동 지각의 기저 신경망에서 핵심적인 요소로 알려진 STSp 영역의 신경 반응을 측정하였다. 그 결과, STSp는 피험자가 생물적 중요성을 지니는 사건을 실제로 지각할 때에만 활성화되고, 이러한 사건이 의식적으로 자각되지 않을 때에는 활성화되지 않음을 발견하였다. 본 연구의 결과는 등 쪽과 배 쪽 시각 정보 처리 경로의 합류 지점에 위치한 STSp 영역이, 생물적 중요성을 지니는 사건의 의식적 지각에 긴밀히 관여할 것이라는 가설을 지지하는 최초의 직접적인 증거로서 그 의의를 지닌다.

주제어 : 생물형 운동, 양안 경쟁, STSp, 의식적 시자각, fMRI