Title Page

Title

PERSPECTIVE TAKING IN BLINDNESS: ELECTROPHYSIOLOGICAL EVIDENCE FOR ALTERED ACTION REPRESENTATIONS

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RUNNING HEAD Blindness and motor imagery

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Abstract

It is well established that the mental simulation of actions involves visual and/or somato-motor representations of those imagined actions. In order to investigate if the total absence of vision affects the brain activity associated to the retrieval of motor representations, we recorded the readiness potential (RP), a marker of motor preparation, preceding the execution as well as the motor imagery of the right middle-finger extension in the first-person (imagining oneself performing the movement, 1P) and in the third-person (imagining the experimenter performing the movement, 3P) modes in 19 sighted and 10 congenitally blind subjects. Our main result was found for the single RP slope values at the Cz channel (corresponding likely to the supplementary motor area). No difference in RP slope was found between 1P and 3P in the sighted group, suggesting that similar motor preparation networks are recruited to simulate our own and other people’s actions in spite of explicit instructions to perform the task in 1P or 3P. Conversely, reduced RP slopes in 3P as compared to 1P found in the blind group indicated that they might have used an alternative, non-motor strategy to perform the task in 3P. Moreover, movement imagery ability accessed both by means of mental chronometry and of a modified version of the Movement Imagery Questionnaire (MIQ-R) indicated that blind and sighted individuals had similar motor imagery performance. Taken together, these results suggest that complete visual loss early in life modifies the brain networks that associate with other’s action representations.

Keywords: Motor imagery; Blindness; Movement-related cortical potentials, EEG
INTRODUCTION

Vision is the most highly developed sense in primates and represents the doorway through which a significant part of our knowledge of the external world arises. Permanent visual loss severely affects daily life activities, causing social and economical problems. In 2002, more than 161 million people worldwide were estimated as being visually impaired, of whom about 37 million were completely blind (Resnikoff et al. 2004). In the past years many studies have investigated how blindness affects visual representations in the brain (Arditi et al. 1988; Cohen et al. 1997; Merabet et al. 2005; Sadato et al. 1996, 2002; Théoret et al. 2004). However, much less is known about how motor representations are affected by complete visual loss. We herein aim to contribute to the knowledge of how blindness affects the mental simulation of actions (or “S” states).

It has been suggested that “S” states correspond to any mental state involving action content where brain activity seems to mimic or simulate all aspects of movement execution, except for the absence of any overt motor behavior (Jeannerod 2001). Therefore, investigating “S” states in blind subjects might help to understand how action representations are affected by the total lack of visual information. Among the S states, motor imagery is well established to share the same neural mechanisms that are also responsible for the preparation and programming of actual movements, with minimal or no activation of the motor output (Jeannerod 1994). Evidence on how blindness specifically affects motor imagery was provided by Imbiriba et al. (2006) by showing that somatic (Rodrigues et al. 2003, 2010) and autonomic (Decety et al. 1993, Decety 1996; Guillot and Collet 2005) responses that associate to the mental rehearsal of postural adjustments in blind subjects are affected by the existence and duration of previous visual experience (review in Imbiriba et al. 2010). Besides, blind subjects rely more on vestibular and somatomotor representations than sighted people during locomotor imagery (Deutschländer et al. 2009), and early blindness was shown to affect substantially the reference frame for the
multisensory control of action (Röder et al. 2007). Taken together, these results would argue in favor of blindness-induced specific changes in sensorimotor representations of actions. Surprisingly, however, early blind people was recently shown to figure out actions evoked by sounds by recruiting cerebral networks similar to those activated by action observation in sighted subjects (Ricciardi et al. 2009, but see Alaerts et al. 2011).

One interesting feature of the mental rehearsal of movements is that the volunteers can be asked to imagine a movement in the first person (1P, also called internal, egocentric or kinesthetic) or in the third person (3P, external, allocentric or visual) perspectives (Decety 1996). Employing positron emission tomography (PET), Ruby and Decety (2001) found in sighted subjects that simulating actions in 1P or 3P perspectives engage distinct brain circuits: while both conditions activated the supplementary motor area (SMA), the precentral gyrus, the precuneus and the MT/V5 complex, when compared to 1P, the 3P perspective recruited the right inferior parietal, precuneus, posterior cingulate and frontopolar cortex, and the opposite contrast revealed activation in the left inferior parietal and somatosensory cortex. In another line of evidence, Sirigu and Duhamel (2001) found that a simple change in the imagery instructions (1P vs. 3P) in a laterality judgment task lead to changes in response time. In addition, selective damage in motor and visual cortices impaired motor and visual imagery, respectively, indicating that under instructions to seek the solution using imagery in the 1P, one would use primarily motor resources, whereas to seek the solution using imagery in the 3P, one would use primarily visual resources.

Subsequent to these seminal works, a plethora of behavioral (Anquetil and Jeannerod 2007), neuroimaging (Guillot et al. 2009; Jackson et al. 2006; Lorey et al. 2009; Solodkin et al. 2004), electrophysiological (Neuper et al. 2005) and transcranial magnetic stimulation (TMS) (Fourkas et al. 2006a, 2006b; Stinear et al. 2006) approaches led to controversial results about the independent nature of these two imagery modes in sighted subjects. Moreover, even when it
refers to “pure” motor tasks, mentally simulating an action in the 3P mode often also implies inferring about other’s intentions (Frith and Frith 2006; Ruby and Decety 2001) and self/other distinctions (Daprati et al. 1997; Jeannerod and Pacherie 2004).

While sighted people are able to use visual imagery to represent tangible objects, including their own bodies, and the space (Parsons 1994), the existence of such ability in blind subjects was at first controversial. Early studies indicated a larger delay for image formation in blind subjects as compared to sighted ones (Kerr 1983; Marmor 1977). It has also been proposed at that time that blind subjects might rely on other imagery modalities or use semantic representations to perform these imagery tasks (Zimler and Keenan 1983). However, the way congenitally blind subjects represent to themselves another person’s action is still controversial (Alaerts et al. 2011; Bedny et al. 2009; Ricciardi et al. 2009). Testing their capacity of imagining an action in 1P versus 3P mode is thus a probe for the important ability of interacting with somebody else's actions and intentions (Jackson et al. 2006; Ruby and Decety 2001).

Does the mental rehearsal of simple actions performed in first and third person modes draw from similar sensorimotor resources? Are these representations affected by the total lack of visual experience throughout life? In this study we wished to (1) further the understanding on the neurophysiological basis of the mental rehearsal of movements when it comes to perspective taking (2) unveil how early blindness affects the mental simulation of movements in 1P and 3P modes. For this purpose we measured the readiness potential (RP), an electrophysiological marker of motor preparation (Deecke 1969), preceding the execution and the mental simulation of a simple finger movement task performed in the first person (1P) and third person (3P) perspectives in sighted in congenitally blind subjects (CBS).
METHODS

Participants

Ten congenitally blind (mean age 25.8 (SD: ± 4.1) years) and nineteen sighted adults (mean age 23.6 (± 2.2) years) participated of this study. The handedness of each subject was assessed by the Edinburgh Inventory (Oldfield 1971), and using an adapted version for the blind volunteers. All participants were male and right-handed (mean laterality index: 0.78 (± 0.29) for blind and 0.83 (± 0.09) for sighted subjects). All subjects were blindfolded during the whole experimental session. Blind subjects reported having no pattern discrimination capacities and at most minimal light perception. Total congenital blindness was of peripheral etiology in all cases: glaucoma (n = 4); optic nerve damage (n = 2); cataract (n = 2); and others (n = 2). Informed consent was obtained from the subjects prior to the experiment, which was carried out according to the local ethics committee standards laid down in the Declaration of Helsinki. All documents were read aloud by the experimenters. Afterwards, volunteers sat in a reclining lounge chair located in a sound attenuated, electrically shielded, and dimly lighted room.

Motor imagery ability

In order to assess movement imagery ability, the volunteers performed the revised version of the Movement Imagery Questionnaire (MIQ-R) (Hall and Martin 1997). Briefly, the MIQ-R assesses visual and kinesthetic movement imagery ability and comprises arm, leg and whole body movements. The participants were first requested to perform and then imagine the same movement. A modified version of the MIQ-R was employed where the two subscales (visual and kinesthetic) were substituted by the following instructions: 1) they should feel themselves doing the action (first-person perspective) or imagine someone else performing the movement (third-person perspective). Afterwards they rated the easiness of generating each motor image on a 7-point scale from 1 = very hard to see/feel to 7 = very easy to see/feel.
Movement duration was also recorded whereas the subjects performed/imagined these movements in the first-person and in the third-person perspectives. The time taken to imagine the movements was measured using a stopwatch and compared with that employed to physically perform the same action. The subjects verbally indicated the start and the end of the trial. An index taking into account the duration of executed and imagined movements in the motor tasks was calculated as follows: \[
\frac{\text{Execution} - \text{Imagination}}{\text{Execution} + \text{Imagination}} \times 100
\]. Negative values indicate that volunteers underestimated and positive values, overestimated movement duration in the motor imagery condition.

**Electrophysiological recordings**

Considered as an expression of the brain preparatory activity preceding voluntary movement execution, movement-related or readiness potentials (RP) consist in slow negative changes in the EEG activity starting as early as 1 to 2 seconds prior to the onset of the electromyographic (EMG) activity in a prime mover muscle (Deecke 1969). When driven by external markers (such as sounds or visual cues), this preparatory activity is often referred to as contingent negative variation (CNV) (Walter et al. 1964). As the EEG component related to the second “imperative” (or starting) cue in CNV paradigms resembles the RP preceding self-paced movements, these two electrophysiological markers are often considered similar (Ikeda et al. 1997; Jankelowitz and Colebatch 2002).

We recorded the RPs preceding an auditory cue associated to the execution or the mental simulation of right middle-finger extensions in 1P and 3P perspectives for both sighted and CBS, in a blocked design. Fifty five auditory cues were presented per block with unequal probability: 90% standard sound vs. 10% rare sound (catch trials). A high pitch served as frequent standard sound (1000 Hz, 70 dB SPL). A low pitch served as rare sound (300 Hz, 70 dB SPL). Catch trials were included to enhance volunteer's alertness. These trials were discarded from further analyses. No comparison was made between catch trials and standard
trials due to the small number of events in the former case. Volunteers were told that they would participate in a task involving mental simulation and execution of movements of the right hand middle finger. They were informed that a frequent sound would mark the moment in time when they should start to imagine or execute the movement. They were also told that there would be three blocks: in the first block they would perform the action; in the second, they should feel themselves extending the right middle finger, and in the third block, to imagine someone else performing this action. Each specific instruction was reinforced before the corresponding block. Subjects were asked to imagine themselves (first-person perspective) or another person (third-person perspective) doing the extension of the right middle-finger after the standard sound. Subjects were instructed to avoid movement execution or imagination in rare sound trials. The order of the two imagination conditions was counterbalanced between subjects. Before each block, a number of training trials were presented to the participants until they felt confident enough that they could perform the task. All auditory stimuli lasted 100 ms and were presented employing the Presentation (NEUROBEHAVIORAL SYSTEM, USA) software. The interval between the stimuli varied randomly between 4500 and 4700 ms to enhance task attentional demand.

EEG activity was recorded from 20 electrode sites, according to the international 10–20 system, using thin silver electrodes referenced to linked earlobes with a forehead ground (impedance below 7 kΩ). All signal analyses were based on the electrical activity over a priori selection of region of interest overlying the primary sensory and motor areas. Besides, the effect of motor imagery strategy was evaluated only in the electrodes that showed an evident RP in the execution condition. Thus, Fz, Cz, C3, C4, Pz, P3, P4 and Oz electrodes were analyzed herein. The EEG was recorded at a sampling rate of 600 Hz (EMSA Medical Instruments, Brazil). The bandpass filter was set between 0.016 and 35 Hz. Trials with artifacts exceeding 100 µV (contaminated by eye blinks or movements) were excluded from further analysis in all channels.
After artifact rejection the minimum number of valid trials per block was 43. Signal was averaged into epochs ranging from 2100 ms before auditory stimuli presentation and 1000 ms afterwards, and the first 100 ms of each epoch were used for baseline correction (2100 to 2000 ms prior to standard sound).

Simultaneously, we acquired the EMG signal from the extensor digitorum communis muscle to register the beginning of movement during execution and to ensure that no overt movement was present during the imagery conditions. Surface electrodes (Ag-AgCl; 8 mm diameter and 2 cm inter-electrode distance) were positioned over that muscle's belly following standard protocol (Jabre et al. 1983). EMG signals were collected by means of a BIOPAC system (model: MP100; A/D conversor of 12 Bits; sampling frequency: 1000 Hz) and a common trigger was used to synchronize acquisition system of physiological data with the sound presentation (See Figure 1 for further details).

**Subjective report**

Obtaining subjective reports in order to assess the quality of the experienced imagery concluded the experimental procedures. The subjects rated the easiness/difficulty with which they were able to do the mental tasks in 1P or 3P perspective. For this question, volunteers marked one answer along a five-point scale [very easy (5); easy (4); not easy nor hard (3); hard (2) or very hard (1)].

**Data analysis**

All physiological signals (EMG and EEG) were segmented and averaged off-line. The following measures were calculated of the RP: (1) gradient of the fitted linear regression between 1 s and 0.1 s prior to the auditory cue (see Jankelowitz and Colebatch, 2002 for further details) and (2) mean amplitude during the same period. These authors have shown that RPs during imagined movements usually start 1 s prior to the cue. RPs were also analyzed by
separating the two classical components (early and late potentials) in the channels of interest (Cunnington et al. 1996; Shibasaki and Hallett 2006). These two windows of analysis encompassed the following time intervals: 2.0 s to 0.5 s (early component) and 0.5 s to 0.1 s (late component) before the sound cue.

For EMG analysis, the difference between the post-stimuli and pre-stimuli periods in three conditions (execution, first- and third-person motor imagery) was computed based on the root mean square of the EMG.

This experiment was designed to investigate differences in RP when imagining the same action in different perspectives (1P or 3P). Therefore our analysis did not include the execution condition. Comparing RPs associated with imagined movements allowed analyzing specifically the motor planning components (Cunnington et al. 1996). RP slopes and mean amplitude values were analyzed by means of a two-way repeated-measures analysis of variance (ANOVA), with "task" (1P and 3P) as a within-subjects factor and "group" (blind or sighted) as a between-subjects factor for each channel separately (Fz, Cz, C3, C4, Pz, P3, P4 and Oz). Moreover, Greenhouse–Geisser correction was applied in function of non-sphericity of variance and post hoc comparisons were made with the Newman-Keuls test. Additionally, Pearson's correlation coefficient was computed between slope and mean amplitude RPs recorded in Cz channel and subjective reports during motor imagery (1P and 3P conditions) both for single or two components of the RPs.

RESULTS

Motor imagery ability

All volunteers were considered as good imagers, as they rated scores higher than 19 points in the MIQ-R in each modality (Guillot et al. 2009). Groups also did not differ in MIQ-R
scores \[F(1, 27) = 0.26, p=0.61\], but there was a task effect: 1P was considered easier to
imagine than 3P \[F(1,27) = 6.61, p=0.01\]. There was no significant interaction between group
and task \[F(1, 27) = 0.42, p=0.52\] (Table 1).

The mental chronometry index in 1P and 3P perspectives also did not differ between
groups \[F(1, 27) = 3.26, p=0.08\] (Table 1). There was no effect of condition or group by
condition interaction \[F(1, 27) = 4.86, p=0.06\], hence demonstrating that the two groups did not
differ significantly in their ability to imagine the movements in the different perspectives.
Interestingly, for both groups and in both imagery strategies there was a trend towards
underestimating the duration of mentally simulated actions.

**Electrophysiological recordings**

The analysis of the brain activity preceding the mental simulation of the right middle-
finger extension in the 1P and 3P perspectives was performed in Fz, Cz, C3, C4, Pz, P3, P4 and
Oz channels (figures 2 and 3).

For the single RP component (between 1 s and 0.1 s prior to the auditory cue),
comparison of slope values in Cz channel revealed a main effect of task \[F(1, 27) = 6.37;
p=0.01\], where participants had smaller slopes in the 3P than in 1P perspective. There was no
main effect of group \[F(1, 27) = 0.02; p=0.88\] but an interaction between groups and tasks \[F(1,
27) = 5.48; p=0.02\]. Post hoc analysis revealed that 1P and 3P imagery modes differed only in
the blind group (\(p<0.05\)). In the sighted group there was no difference between conditions
(Figure 4). Moreover, comparison of slope values at C3, C4 and P4 channels have shown only a
main effect of task (\(p<0.05\)), where participants had smaller slopes in the 3P than 1P condition.
No other global differences were found (table 2).

Further, analysis of the RP mean amplitude revealed that there was no effect either of
group, task or group-by-condition interaction for all the analyzed channels (table 3). The results
showed that RP slope was more robust than mean amplitude in identifying cerebral activity
during introspective states of action simulation. These parameters seem to reflect different
aspects of the EEG activity. For movement-related conditions, RP slope reflects the increase in
neural activity associated with motor preparation (Cunnington et al. 1996). On the other hand,
mean amplitude is a mean point taken during this same period and, for this reason, less
representative of the raw signal.

Additionally, RPs were analyzed by separating the two components (early and late
potentials) in the channels of interest. A two-way ANOVA of both parameters (mean amplitude
and slope) revealed that there was no effect either of group, task or group-by-condition
interaction (p > 0.05) for all the analyzed RP components (early and late).

A significant task effect (F(2,54) = 62.37; p<0.0001) was found when the difference
between post and pre movement EMG activity was computed: as expected, this difference was
higher in the execution condition than in both imagery conditions. The absence of any group
effect (F(1,27) = 2.67; p=0.11) and of any interaction [F(2,54) = 2.16; p=0.12], ensured that no
overt movement was present during the imagery conditions for both groups. These results
showed that the muscles, which are normally involved in the execution of an action, remained
silent during the mental simulation of this action both in 1P and in 3P perspectives.

**Subjective report**

There was no difference between groups (p=0.156) in the evaluative report for imagining
the finger extension in 1P and 3P, nor interaction between group and task, but there was a trend
of a task effect (p=0.078), where 1P (3.6 ± 1.04) was considered easier to perform than 3P (3.1 ± 1.25) for both groups.

Finally, there was no significant correlation between RP slopes (correlation coefficient
range: 0.01 to 0.36, p>0.05) and mean amplitudes (correlation coefficient range: 0.05 to 0.23,
p>0.05) versus subjective reports in 1P and 3P for both groups.
Movement imagery ability accessed both by means of mental chronometry and of a modified version of the Movement Imagery Questionnaire (MIQ-R) (Hall and Martin 1997) indicated that CBS and sighted individuals had a similar motor imagery quality in 1P and 3P perspectives. This analogous performance between groups is in accordance with previous reports showing that CBS are able to perform visual-spatial imagery tasks, with some aspects of mental imagery being evoked by multiple modalities (for example, auditory, tactile and haptic) and stored as abstract representations (Arditi et al. 1988; Cattaneo et al. 2007, 2008; Lambert et al. 2004; Monegato et al. 2007; Vanlierde and Wanet-Defalque 2004).

Readiness Potential (RP) slope values (between 1 s and 0.1 s prior to the auditory cue) of similar magnitude were recorded in sighted subjects at the Cz channel during motor imagery of the right middle-finger extension in 1P and 3P perspective. Conversely, reduced RP slopes in 3P as compared to 1P found in the blind group indicated that they might have used an alternative, non-motor strategy to perform the task in the 3P perspective.

RPs were further analyzed by separating the two classical segments (early and late potentials) and no effect of group, task and component nor any interaction was found in the channel of interest. Thus, contrarily to RPs associated to execution, when it comes to imagined movements, it seems not possible to separate preparatory and execution-related components within the RP signal (Cunnington et al. 1996). Indeed, motor imagery-related RPs are described as symmetrical and largest at Cz channel with no definite early and late components (Jankelowitz and Colebatch 2002). Interestingly, regression of these RP reveals r-values for a single line adjustment that are always higher than for two RP (early and late) components, suggesting that the former approach results in a best fit when it comes to motor imagery (Jankelowitz and Colebatch 2002).
Studies employing EEG source localization and functional neuroimaging during the preparation, readiness, and execution of purely self-initiated voluntary movements (Ball et al. 1999; Cunnington et al. 2005; Jahanshahi et al. 1995; Nachev et al. 2008) found activation within frontal mesial areas, including supplementary (SMA) and cingulate motor areas, providing evidence that these areas play an important role in the building of voluntary movements. Likewise, Cunnington et al. (1996) and Jankelowitz and Colebatch (2002) reported that RPs related to movement imagination were largest at Cz. Accordingly, similar RP values recorded at Cz channel in 1P and 3P perspectives in sighted subjects and in 1P in CBS indicate that they might have recruited motor areas. In sighted subjects this occurred irrespectively of the strategy, confirming that the representations used to simulate the action of another person must be close to those built for performing that same action (Anquetil and Jeannerod 2007; Fourkas et al. 2006a, 2006b). Thus, in normal volunteers, motor imagery performed in 3P also draws itself from their own motor resources (Ruby and Decety 2001), at least when it comes to simple motor tasks and in spite of explicit instructions prior to each condition to concentrate on specific visual or kinesthetic information.

In CBS, when it comes to brain activity preceding motor execution, Fiehler et al. (2009) found greater activation than the sighted group in the presupplementary motor area and right precuneus during a kinesthetically guided hand movement. Likewise, Lehtokoski et al. (1998) showed that the RP preceding a self-paced movement is enhanced in blind subjects, maybe reflecting an increased motor-tactile rehearsal loop. In the present study, a RP was identified during motor imagery performed in 1P in CBS, indicating that, as for sighted subjects, similar networks from those of execution are at play.

Additionally, functional imaging studies in early blind subjects indicate that the visual cortex can be recruited for the sensory processing of tactile and auditory input (Amedi et al. 2004, for a review see Théoret et al. 2004). For example, tactile input from reading Braille or
discriminating between complex tactile patterns activates the visual cortex almost as much as the sensorimotor cortex (Cohen et al. 1997; Sadato et al. 1996). Our results for parieto-occipital electrodes showed, however, no brain potential distribution differences between sighted and CBS groups. Thus, the cortical control of motor functions in CBS, at least, evaluated by the RP amplitude and slope parameters, does not spread into cortical areas normally serving the visual modalities (Lehtokoski et al. 1998).

Conversely to what was found for the sighted group, no slope negativity was found in the 3P mode at Cz channel in CBS. Thus, for this group, motor planning and execution occur likewise in 1P but not in 3P mode. It is well established that mental simulation of an action brings forth stored sensorimotor representations (Jeannerod 2001; Parsons and Fox 1998), providing an estimate of the sensory consequences of the simulated movement (Wolpert et al. 2001).

Results from behavioral studies in normal subjects and patients with brain lesions suggest that the mechanisms mediating imagery in the first and in the third person are somewhat different (Jackson et al. 2006; Rodrigues et al. 2010; Sirigu and Duhamel 2001). Accordingly, different cortical networks are recruited when one directly compares metabolic activity emerging from tasks performed in first and third person perspectives (Ruby and Decety 2001). Herein subjects were instructed to “feel” themselves performing the movement in the first person perspective. In this case, internal or kinesthetic imagery is expected to be employed, possibly implying mostly sensorimotor networks (Lorey et al. 2009; Solodkin et al. 2004; Stinear et al. 2006). On the other hand, in sighted subjects the third person perspective leads to the recruitment of more visual-related structures (Guillot et al. 2009; Jackson et al. 2006; Ruby and Decety 2001; Sirigu and Duhamel 2001).

One has to keep in mind that CBS have never experienced the sight of their own or of other people’s actions. Early blindness should thus conceivably correlate with changes in motor representations, especially those related to the imagery performed in a 3P (allocentric) mode.
Röder et al. (2004, 2007) has shown that late but not congenitally blind people are impaired in tactile discrimination tasks when they cross their hands, suggesting the critical role played by childhood vision in modulating the perception of touch that may arise from the emergence of specific cross modal links during development, and indicating that behavioral outcome very critically depends on early childhood vision. In accordance with this proposal, our results further indicate that early blindness also affects the mental representation of body movements performed by others.

The fact that congenitally blind children may display autism-like characteristics (Hobson and Bishop 2003; Théoret and Fecteau 2005) and perform at lower levels than normal subjects on theory-of-mind tasks (Minter et al. 1998) have been taken as evidence that the normal mechanism matching action-perception and execution within the visual system (Rizzolatti and Craighero 2004) could be derailed in early blind individuals (Théoret and Fecteau 2005). A motor resonance mechanism could still operate through the auditory modality (Kohler et al. 2002; Lahav et al. 2007), but in an obviously limited manner. However, recent studies have revealed that the pattern of brain activation emerging from reasoning about mental states based on visual information is similar in congenitally blind and sighted individuals (Bedny et al. 2009). Likewise, blind people were shown to figure out the actions evoked by sounds by recruiting similar cerebral networks that are activated by action observation in sighted subjects (Ricciardi et al. 2009). The authors further suggested that this system is based on supramodal sensory representations of actions which would allow individuals with no visual experience to interact effectively with others. Measuring TMS cortico-motor facilitation while subjects passively perceived manual actions (either visually or aurally), Alaerts et al. (2011) showed however that congenitally blind subjects displayed substantially lower resonant motor facilitation upon action perception compared to sighted subjects, suggesting that action perception in blind subjects...
engages a mode of action processing that is different from the human action recognition system recruited in typically developed subjects.

As mentioned before, in the visual-spatial imagery (Arditi et al. 1988; Cattaneo et al. 2008; Dulin et al. 2008; Vanlierde and Wanet-Defalque 2004), a motor imagery task in the 3P perspective in CBS could possibly be performed through the recruitment of the remaining modalities (for example, auditory, tactile and haptic), stored as abstract representations. Besides, Bedny et al. (2009) also proposed that CBS can understand someone else's experience and share its more abstract features (e.g. sounds, emotions and environment) by learning from what he (she) says about his (her) own states (language). In any case, mental simulations are almost certainly never exact re-enactments of previously experienced category instances and the level of detail may vary widely, from being relatively vague to vivid and detailed depending on the amount of information available or required (Barsalou 2009).

Our results in CBS indicate that, when it comes to a simple, intransitive movement with no sound-associated motor representations (Lahav et al. 2007; Ricciardi et al. 2009), the brain activity that associates to the mental representation of body movements performed by others departs from those evoked during the mental simulation of their own movements, and point to a non-motor strategy in the 3P mode. In sighted subjects, besides the existence of common (mostly sensorimotor) cortical areas activated in 1P and 3P modes, the 3P perspective further recruits the right inferior parietal, precuneus, posterior cingulate and frontopolar cortex when compared to 1P (Ruby and Decety 2001). Further studies are necessary to unveil which brain networks are recruited in order to build a 3P representation in CBS, but our results suggest the existence of an alternative (non–visual, non somato-motor) route at play to perform this task (Rumiati et al. 2010).

One clear limitation of the above cited approaches is the fact that the experiments are often devised by sighted people, most probably imposing a visual default to the tasks (see also
Arditi et al. 1988; Bedny et al. 2009) and creating an additional task demand for the blind group. While the 3P motor imagery task (generating a 3P motor image of a finger extension) can be considered as relatively simple for sighted subjects, this task might possibly be much more demanding, and probably draw on higher order cortical resources in CBS. In other words, one possibility is that this load effect would induce a change in the brain networks from the primary sensorimotor areas towards higher order cortical regions when the task is to be performed in the 3P mode.

In summary, this study highlights the presence of preparatory slow brain potentials in the scalp region corresponding most likely to the SMA complex prior to movements either executed or imagined in 1P mode both in sighted and blind subjects. This cortical region was activated during motor imagery in 3P perspective in sighted but not in CBS, suggesting that early blindness might lead to changes in motor representations associated to movement performed by others. There are still important gaps on the consequences of visual loss upon motor control and future studies might be necessary to further investigate how blindness relates to changes in the higher order aspects of action planning.

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Disclosures

The authors declare no conflict of interest

REFERENCE LIST


Table 1. Motor imagery abilities

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<th>Blind subjects (n=10)</th>
<th>Sighted subjects (n=19)</th>
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<td>1P</td>
<td>3P</td>
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<tr>
<td>Motor Imagery Questionnaire (min: 4 – max: 28)</td>
<td>21.4 (± 8.56)</td>
<td>19.1 (± 7.51)</td>
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<td>Mental chronometry index (%)</td>
<td>-10.3 (± 10.2)</td>
<td>-9.1 (± 8.9)</td>
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Table 2: Mean Amplitude Values

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<th></th>
<th>Blind subjects</th>
<th></th>
<th>Sighted subjects</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(n=10)</td>
<td></td>
<td>(n=19)</td>
<td></td>
</tr>
<tr>
<td>Fz</td>
<td>-3.32 (4.92)</td>
<td></td>
<td>-2.22 (3.78)</td>
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</tr>
<tr>
<td>C3</td>
<td>-1.84 (3.73)</td>
<td></td>
<td>-1.89 (3.38)</td>
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<tr>
<td>Cz</td>
<td>-1.64 (6.29)</td>
<td></td>
<td>-3.05 (5.19)</td>
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<tr>
<td>C4</td>
<td>-1.61 (3.39)</td>
<td></td>
<td>-1.54 (3.39)</td>
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<tr>
<td>P3</td>
<td>-0.35 (3.03)</td>
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<td>-0.25 (3.17)</td>
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<tr>
<td>Pz</td>
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<td>-1.41 (4.17)</td>
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<tr>
<td>P4</td>
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<td>-0.35 (2.63)</td>
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<tr>
<td>Oz</td>
<td>-1.02 (3.77)</td>
<td></td>
<td>0.59 (4.18)</td>
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<td></td>
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<td></td>
<td>-0.55 (2.29)</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>1.51 (4.99)</td>
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## Table 3: Slope Values

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<td>(n=19)</td>
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<tr>
<td>1P</td>
<td>3P</td>
<td>1P</td>
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<tr>
<td>Fz</td>
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<td>C4</td>
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<tr>
<td>Oz</td>
<td>0.82 (1.99)</td>
<td>-0.85 (0.84)</td>
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Figure Captions.

Figure 1. Schematic representation of the experimental design. (a) Adopted posture of participants; (b) experimental situations: execution or motor imagery (first person or third person) of the right middle-finger extension movement and (c) representative data from one participant (blind group) depicting the physiological signals acquired during execution, first-person (1P) imagery and third-person (3P) imagery of left finger extension. Readiness potential (upper) and rectified electromyographic (EMG) signal (lower).

Figure 2. Topographical representation of the electrophysiological recordings in congenitally blind subjects (CBS) during the experimental conditions: first-person (1P) and third-person (3P) imagery. Readiness potentials are shown from 2.1 s before to 1 s after the sound cue.

Figure 3. Topographical representation for electrophysiological recordings in sighted group during the experimental conditions: first-person (1P) and third-person (3P) imagery. Readiness potentials are shown from 2.1 s before to 1 s after sound cue.

Figure 4. a) Data of representative volunteers depicting the analysis windows for readiness potentials (RP) during motor imagery conditions. b) RP mean slope of the line of best fit averaged during motor imagery in different perspectives (first-person (1P) or third-person (3P)) for Cz channel in blind and sighted group in the time interval between 1 s and 0.1 s prior to the auditory cue (* significant differences between conditions, p<0.05).
Table 1. Movement imagery questionnaire scores and mean percentage differences between imagination and actual movement duration in blind and sighted groups during the first-person (1P) and third-person (3P) perspectives. Mean values and standard deviation for all analyzed parameters were computed.

Table 2. Mean amplitude (standard deviation) of the readiness potential, in the time interval between 1 s and 0.1 s prior to the auditory cue, in each analyzed channel for the experimental conditions: first-person (1P) and third-person (3P) imagery. All values in µV.

Table 3. Mean slope (standard deviation) of the readiness potential, in the time interval between 1 s and 0.1 s prior to the auditory cue, in each analyzed channel for the experimental conditions: first-person (1P) and third-person (3P) imagery. All values in µV/s.
Electroencephalographic recording (Cz channel)

Electromyographic recording (EMG)

(a) Block 1: execution

First-person perspective (1P)
Third-person perspective (3P)

Blocks 2/3 (randomized) Motor imagery

c) Electroencephalographic recording (Cz channel)

Electromyographic recording (EMG)
Sighted subjects

Tasks: 3p 1p
a) 

**blind**

-20 -15 -10 -5 0 5 10 15 20

**sighted**

-20 -15 -10 -5 0 5 10 15 20

b) 

**Cz channel**

![Diagram showing mean amplitudes and time courses for different conditions and groups.](image-url)