Transcranial magnetic stimulation of posterior parietal cortex affects decisions of hand choice

Flavio T. P. Oliveira[a,b,1], Jörn Diedrichsen[c], Timothy Verstynen[d,e], Julie Duque[f], and Richard B. Ivry[a,b]

[a]Department of Psychology and [b]Helen Wills Neuroscience Institute, University of California, Berkeley, CA 94720; [c]Institute of Cognitive Neuroscience, University College London, London WC1N 3AR, United Kingdom; [d]Center for the Neural Basis of Cognition and [e]Learning Research and Development Center, University of Pittsburgh, Pittsburgh, PA 15260; and [f]Institute of Neuroscience, Université Catholique de Louvain, B-1200 Brussels, Belgium

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Deciding which hand to use for an action is one of the most frequent decisions people make in everyday behavior. Using a speeded reaching task, we provide evidence that hand choice entails a competitive decision process between simultaneously activated action plans for each hand. We then show that single-pulse transcranial magnetic stimulation to the left posterior parietal cortex biases this competitive process, leading to an increase in ipsilateral, left hand reaches. Stimulation of the right posterior parietal cortex did not alter hand choice, suggesting a hemispheric asymmetry in the representations of reach plans. These results are unique in providing causal evidence that the posterior parietal cortex is involved in decisions of hand choice.

decision making | motor control | manual reaching | action

Interacting with the world requires continuously making decisions about possible courses of action. Although these decisions appear to occur seamlessly, they are the product of complex computations that take multiple factors into account. Considerable attention has been given in the psychological and neuroscience literature to the study of perceptual decisions. In many studies, participants decide which category best describes a perceptual stimulus and researchers record single-cell activity in monkeys (1–3) or hemodynamic responses in humans (4, 5). Other studies have looked at motor-related decisions: for example, when an animal is to reach to one of multiple targets (6, 7) or when a response can be produced with either a hand or eye movement (8, 9).

Notably, few studies have examined one of the most commonplace decisions humans make: which hand should be used to perform an action (10–12)? Consider the relatively simple decision required in choosing whether to use the left or right hand to press an elevator button. Although this decision appears to require minimal conscious thought, it is influenced by past experience, the current positions of the hands, and the spatial location of the button. Informal observation indicates people flexibly use either hand to perform unimanual actions of this type. However, a characterization of this fundamental decision process, as well as insight into the underlying neural mechanisms, has received minimal attention in the literature.

Traditional psychological theories postulate that decisions arise through a serial process involving perception, cognition, and action as independent hierarchical processes (13–16). With respect to hand selection, this approach has emphasized that decisions are made at a cognitive, effector-independent level, with the output engaging the motor system to implement the selected action. In contrast, computational and neurobiological approaches view decision-making as a bounded accumulation process (5, 17, 18). In the context of hand selection, such models would assume that neural activity related to the planning and preparation of a response would entail a competitive decision process between simultaneously activated action plans for each hand. Once activity for one of the plans reaches a threshold, the selected response is initiated. This view emphasizes that decisions are made through an integrative parallel process that binds perception, cognition, and action (5, 17, 19, 20).

Converging lines of evidence support the idea that decisions about hand selection emerge through simultaneous activation of competing action plans. One source of evidence comes from the "alien hand syndrome" in which a patient may produce a goal-directed movement with one limb while denying having conscious control over it. In some cases, these patients may inadvertently produce reaching movements with both hands, even when instructed to use only one hand (21). Alien-hand syndrome is commonly observed in patients with lesions or resection of the corpus callosum (22), suggesting an impairment in resolving the competition between multiple, lateralized action plans. Another striking example of parallel planning comes from a study showing the inadvertent production of multiple precued movements following an unexpected and startling sound (23).

Several studies point to a critical role for the posterior parietal cortex (PPC) in planning reaching movements. Lesions of the parietal lobe can result in optic ataxia, a condition disrupting visually guided reaching with the contralesional hand (24). Neurophysiological studies with monkeys (25, 26) and neuroimaging studies with humans (5, 27, 28) also emphasize a critical contribution of the parietal lobe in reach planning. Indeed, the functional term "parietal reach region" has been coined to highlight the role of a subregion of the PPC in reaching. However, although this work has emphasized the importance of the PPC in movement planning, the contribution of this region to the selection of reaching movements remains unclear.

Here we examine the decision process associated with hand choice during unimanual reaching movements. To investigate this decision process we introduce a new task, in which participants were asked to reach with one hand to a visual target that appeared at a variable location on a semicircular array. The first behavioral experiment had different blocks in which the reaching hand was either predetermined (left hand-only or right hand-only blocks) or the participant was free to choose the right or left hand. In the latter condition, we were able to identify targets where decision uncertainty was minimal (i.e., the participant always used the same hand) and targets where uncertainty was maximal (i.e., the participant chose the right and left hand with approximately equal probabilities). Based on competitive bounded accumulation models (1, 2, 18, 29, 30), we expected reaction times (RTs) would be longer for decisions involving high uncertainty.

To evaluate the hypothesis that the PPC has a causal role in hand selection, we conducted a second experiment using transcranial magnetic stimulation (TMS). Although neuroimaging studies typically reveal bilateral PPC activation during unimanual movements, the activity is generally stronger in the hemisphere contralateral to the selected hand (27, 31–33). This pattern is

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[1]To whom correspondence should be addressed. E-mail: oflavio@gmail.com.

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consistent with the idea that PPC activity levels reflect a competitive process related to hand selection. We assumed that TMS over PPC would disrupt the accumulation process associated with preparing a reach with the contralateral hand. As such, we hypothesized that TMS would lead to an increase in the probability that the reach would be performed with the hand ipsilateral to the stimulation site. To identify nonspecific effects of TMS stimulation, we conducted a follow-up control experiment in which TMS was targeted at two lateralized control regions.

Results

Experiment 1: Effect of Hand Competition on RTs. In experiment 1, we asked participants to perform unimanual reaches as fast and as accurately as possible under three different conditions. For two of those conditions (RIGHT-ONLY and LEFT-ONLY), the response hand was predetermined and fixed for the entire block of trials. For the third condition (CHOICE), participants were free to use either hand on each trial, with the constraint that they were to respond as quickly as possible. Given the semicircular array of targets (Fig. 1*B*), it was possible to construct a psychometric function of hand preference for each participant. As shown in Fig. 2, hand choice followed a sigmoidal pattern across targets, switching from left hand preference to targets on the left side of space, to right hand preference to targets on the right side of space. Using logistic regression, we estimated the point of subjective equality (PSE): the virtual point in space at which participants would have an equal probability of using the right or the left hand for the reach (Fig. 2). The mean PSE was to the left of the midline, at −15.2°. Thus, participants exhibited an overall bias to reach more often with their dominant, right hand.

To evaluate the effect of uncertainty on response preparation, we compared the RT for reaches to extreme targets (lowest uncertainty, i.e., ± 90° relative to the midline) to the RTs for the two targets surrounding the PSE (highest uncertainty, determined on an individual basis). We further separated the RTs of central and extreme targets by hand choice condition, combining the RIGHT-ONLY and LEFT-ONLY conditions to create a single condition in which the hand was predetermined. Overall, RTs were longer in the CHOICE condition than in the PREDETERMINED condition (condition main effect, marginal means = 423 ms vs. 400 ms, $P = 0.0007$), showing that there is a cost associated with hand selection. For the predetermined condition, RTs were faster for the targets around the PSE (defined in the CHOICE condition) than for the extreme targets ($P = 0.014$) (Fig. 3). This result is likely caused by increased deployment of attention to the center of the visual space, an optimal strategy because it would minimize the average distance from the center of attention to the full set of possible targets. Importantly, this pattern of results was reversed for the CHOICE condition (interaction effect: $P = 0.0033$). Here, RTs were significantly longer for the targets around the PSE than for the extreme targets ($P = 0.0039$) (Fig. 3). The increase in RT suggests a cost associated with a competition between the action plans for each hand at locations where ambiguity in hand choice is maximal.

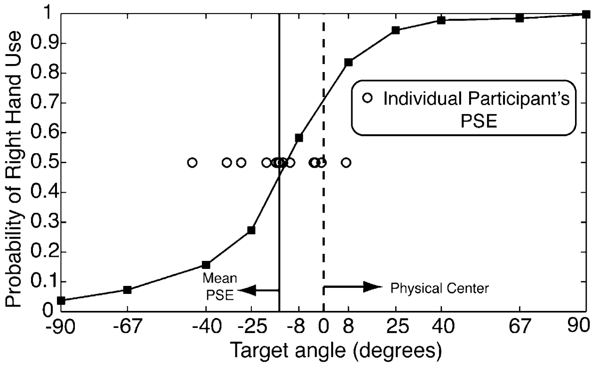

Fig. 2. Psychometric function of hand choice for the CHOICE condition. Mean probability of right hand use is plotted as a function of target location. Targets are listed according to their location, in degrees, relative to the midline (−90, leftmost target; 90, rightmost). The dashed vertical line indicates the physical center of the target array. The solid vertical line represents the mean PSE, the estimated location at which participants were equally likely to use the right or left hand. Circles represent individual participant's PSE.

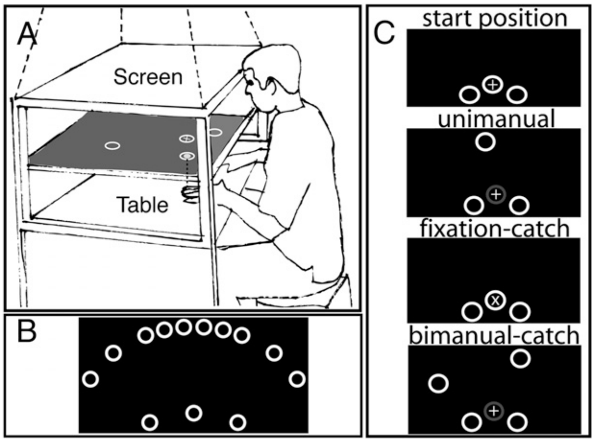

Fig. 1. Schematic illustration of the experimental setup and stimuli. (*A*) An LCD projector presented the stimuli on the top screen. By viewing the stimuli on a mirrored surface placed halfway between the screen and the table surface, participants had the impression that the stimuli were in the same plane as their hands. The position of the hands was indicated by two white dots (not displayed). (*B*) Starting circles (bottom two circles), fixation circle (center circle), and the 10 possible target locations. (*C*) Start position (*Top*) and the three types of trials. On unimanual trials, the participant reached with one hand toward the target. This hand was either predetermined (RIGHT-ONLY and LEFT-ONLY conditions) or was selected by the participant after the onset of the target (CHOICE condition). For bimanual-catch trials, two target circles were presented and the participant reached to each target concurrently using both hands. For fixation-catch trials, the "+" at the center of the fixation circle changed to an "×" and the participants moved both hands to the fixation circle.

Experiment 2: TMS to Left PPC Influences Hand Choice. In experiment 2, we sought to investigate the causal contribution of the PPC in hand selection. Moreover, we sought to directly test the hypothesis that hand choice arises through a competitive process between the left and right PPC. To this end, we applied single-pulse TMS with the expectation that this stimulation would influence hand selection. Participants performed unimanual reaches following the same procedures as in the CHOICE condition in experiment 1. In separate blocks of trials, single-pulse TMS was administered over the PPC of the right (right-PPC) or left (left-PPC) cerebral hemispheres. TMS was applied 100 ms after the target onset, with the stimulation intensity set to 120% of the resting-motor threshold. We also included blocks in which TMS was not administered (no-TMS). Anatomical MRIs were used to identify the target stimulation regions for each participant. The scalp location representing the caudal part of the intraparietal sulcus (IPS), just anterior to the parieto-occipital sulcus, of each hemisphere was identified using a stereotaxic localization system (Fig. 4). We based our stimulation location on neuroimaging evidence showing that this region is consistently activated during reach planning (5, 27, 28, 31, 33).

Similar to experiment 1, we compared RTs for targets around the PSE to RTs for targets at extreme locations, collapsing across the TMS conditions. Replicating the effect found in experiment 1, RTs were slower for targets around the PSE (400 ms) compared

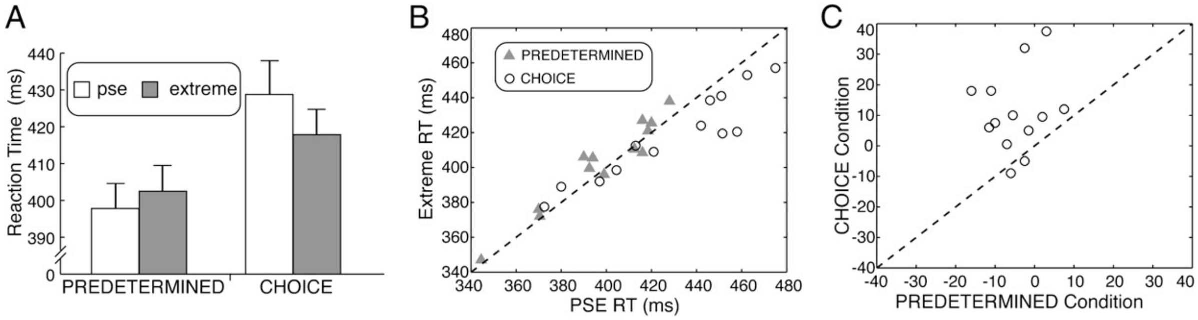

Fig. 3. Effect of target location and hand choice condition on reaction time. (*A*) Mean RTs for the two targets around the PSE and the two extreme targets (PREDETERMINED combines the RIGHT-ONLY and LEFT-ONLY conditions). Error bars represent SE. (*B*) RTs for each participant separated by condition. Each point displays median RT for extreme (vertical axis) and for PSE (horizontal axis) targets. The dashed line represents points in which RTs are the same for extreme and PSE targets. Datapoints in the PREDETERMINED condition (triangles) generally fall above the equality line, showing that RTs for extreme targets were slower (403 ms) than for PSE targets (398 ms; *P* = 0.014). Datapoints in the CHOICE condition (circles) generally fall below the equality line, showing that RTs for PSE targets were slower (429 ms) than for extreme targets (418 ms; *P* = 0.0039). (*C*) RT difference (ms) between PSE and extreme targets. These data were derived by subtracting the RT for the PSE targets from the RT for the extreme targets. Circles represent individual participant data. All but two circles fall above the equality (dashed) line, showing a target location by condition interaction (*P* = 0.0033). Eight out of the 13 circles fall in quadrant one, showing a negative difference (RTs were larger for extreme than for PSE targets) in the PREDETERMINED conditions and a positive difference (RTs were larger for PSE than for extreme targets) in the CHOICE condition.

with extreme targets (388 ms, $P = 0.001$). TMS to PPC also led to marginally reliable increases in RT (left-PPC: 392 ms, $P = 0.0752$; right-PPC: 394 ms, $P = 0.0703$) compared with the no-TMS condition (386 ms).

To test whether TMS influenced hand choice, we calculated the probability of right and left hand movements under the three TMS conditions. Collapsing over all target locations, TMS to left PPC, but not right PPC, led to an increase in the use of the hand ipsilateral to the stimulation site (Fig. 5*A*). Participants had a 4% increase in left-hand use after left-PPC stimulation compared with the no-TMS condition ($P = 0.0244$) and a 5.2% increase relative to right-PPC stimulation ($P = 0.0137$). Because we expected the effect of TMS to be maximal when hand choice competition was highest, we used logistic regression to estimate the change in hand use at the location corresponding to the PSE derived from the no-TMS condition (Fig. 5*C*). When the analysis was restricted in this manner, left-PPC stimulation led to a 13.5% increase in left-hand use relative to the no-TMS condition ($P = 0.0352$) and a 21.5% increase relative to the right-PPC condition ($P = 0.0312$).

These shifts in hand use were also found in a comparison of the PSE location for each condition (Fig. 5*E*). Consistent with what we found in experiment 1, the mean PSE for the no-TMS condition was slightly to the left of the physical center at −20.5° with respect to the midline. The increase in left hand use after left-PPC stimulation led to a rightward shift in the PSE (comparison with no-TMS = 2.7°, $P = 0.0215$; comparison with right-PPC = 3.1°, $P = 0.0156$). As with the other analyses, there was no significant difference between the right-PPC stimulation and the no-TMS conditions.

Given the role of the parietal lobe in spatial attention (34), it is important to consider whether the effects of TMS were related to disruptive effects on attentional processes rather than processes reflecting a competition related to hand selection. If TMS produced a transient form of contralateral extinction (35), one would expect a selective increase in RTs for targets in the visual hemifield contralateral to the stimulated site. Overall, RTs to targets in the right visual hemifield were faster than to targets in the left visual hemifield (388 ms vs. 399 ms, $P = 0.0499$). This finding is likely because of the decreased ambiguity in hand choice for right hemifield targets, as well as the fact that a greater percentage of reaches were performed with the (right) hand ipsilateral to that hemifield, a situation in which visual input and motor output are associated with the same cerebral hemisphere (36). Importantly, this visual field difference was not influenced by the TMS condition ($P = 0.3109$), arguing against an attentional account (Fig. S1).

Controlling for Nonspecific Effects of TMS. We conducted a follow-up control experiment to assess nonspecific effects of TMS that might influence hand selection. We used a similar procedure to that used in the PPC TMS experiment but applied single-pulse TMS over control regions in left or right anterior parietal cortex. Importantly, we found no significant changes in hand preference following stimulation over either hemisphere's control region compared with the no-TMS condition. This null effect held for all three measures of interest (Fig. 5 *B*, *D*, and *F*). Thus, the shift in hand selection observed during left-PPC stimulation does not appear to be related to nonspecific effects of TMS. TMS again led to an increase in RT compared with the no-TMS condition, an effect that was reliable for stimulation over the left hemisphere control site (421 ms vs. 410 ms, $P = 0.0039$; right hemisphere control site RT = 415 ms, P not significant). Combined with the PPC effects, it appears that TMS may produce a small increase in RT for hand choice in a nonspecific manner.

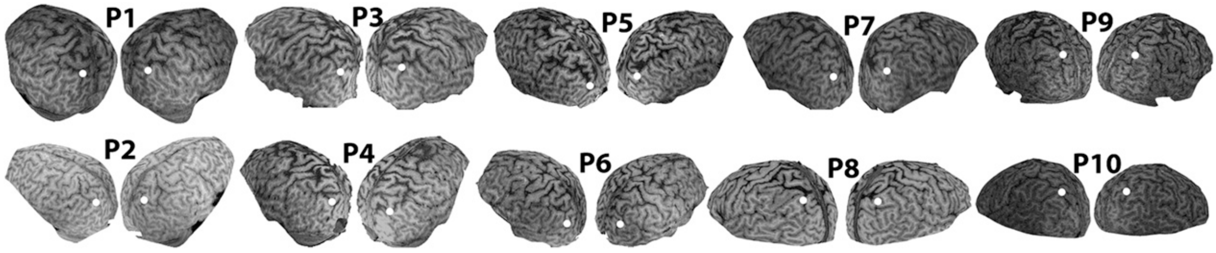

Fig. 4. 3D reconstructions of participants' brains. White dots indicate target stimulation area, defined as caudal part of the IPS.

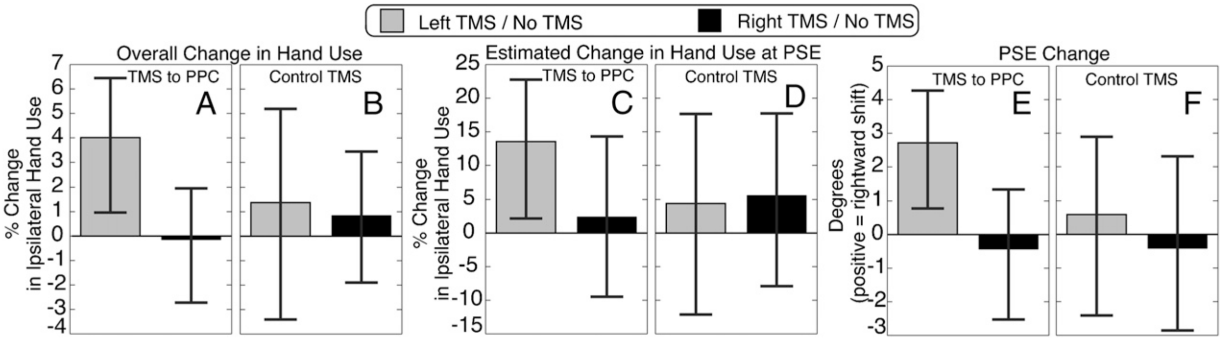

Fig. 5. Effect of TMS on hand choice. (*A* and *B*) Change in hand use over all target locations. Change is expressed as percent-change in ipsilateral hand (increase is positive), measured by calculating the difference in probability of ipsilateral hand use between the TMS condition of interest (left or right TMS) and the no-TMS condition, and then dividing this difference by the probability in the no-TMS condition. Circles represent individual participant data. (*C* and *D*) Estimated change in hand use at the PSE (based on the no-TMS condition). (*E* and *F*) PSE change. Positive numbers represent more left hand use. Error bars represent one-sided 95% upper and lower confidence bounds.

Discussion

The current results shed light on the mechanisms involved in selecting which hand to use when making a unimanual reach. This fundamental decision process appears to involve a competition between action plans associated with each hand. In experiment 1, RTs were longer when participants made unimanual reaches to regions of space where ambiguity about hand choice was maximal, compared with regions of space where ambiguity was minimal (37). This result suggests that the increased competition associated with ambiguous targets entails longer preparation processes, consistent with the predictions of bounded accumulation models (1, 2, 18, 29, 30). Previous work on such models focused on perceptual decisions (2, 4, 5, 18) or on decisions about which target to reach for with a predetermined hand (17). We extend this literature by showing that similar processes appear to govern decisions about hand choice.

Multiple mechanisms might lead to longer RTs under situations of increased competition between the hands. Within accumulator models, high uncertainty can delay decision times by slowing the rate of accumulation (2, 18, 38). This finding could be the result of mutual inhibition between the activated action plans for left and right hand reaches (39–42) or the distribution of limited resources (neural accumulation) between possible responses. An alternative possibility is that the threshold of activity necessary to trigger a response is elevated or the baseline activity is lowered under situations of increased uncertainty; both of these mechanisms can improve the accuracy of choices (1, 2, 18, 43). These possibilities are not mutually exclusive. All predict that neural accumulation under increased competition should take longer to reach the decision threshold.

In experiment 2 we sought to directly test the hypothesis that the PPC is involved in decision processes related to hand choice. By stimulating the caudal IPS, a PPC region associated with reach planning (5, 27, 28, 31, 33), we sought to selectively disrupt the plan associated with the contralateral hand and thus increase the likelihood of an ipsilateral reach. We were able to induce this bias when stimulating the left PPC. Previous TMS studies had implicated more anterior regions of the human PPC in reach and grasp correction (44, 45), suggesting a role of the PPC in reactively updating sensorimotor representations (46). Our study provides causal evidence that the human PPC is also proactively involved in the process of deciding which hand will be used for a manual reach. Indeed, the current study complements and extends previous efforts to use stimulation techniques to influence decision-making. Past research has involved microstimulation in monkey PPC to alter perceptual decisions (3); here, we show that TMS of the human homolog of the parietal reach region can alter a fundamental motor decision.

One concern is that the observed shift in hand use might be related to nonspecific effects of TMS. Two pieces of evidence argue against this hypothesis. First, we only found a change in hand choice in the left-PPC stimulation condition. If nonspecific TMS effects were responsible for such result, then we would have expected a similar effect in the right-PPC stimulation condition. Second, no significant changes in hand choice were observed with either left or right hemisphere stimulation over more anterior parietal control regions.

We did not observe a change in hand use when the stimulation was directed to the right PPC. The source of this unexpected asymmetry remains unclear. One possibility is that this asymmetry reflects limitations in the sensitivity of our methods. Neuroimaging studies generally show smaller reach-related activity in the right PPC compared with the left PPC (32, 47–49). This result suggests that it may be more difficult to reliably target the decision region within the right PPC compared with the left PPC. It is also possible that the absence of an increase in right hand use following TMS to the right PPC is because of the fact that our right-handed participants exhibited a strong bias to use their dominant hand. This baseline bias may have left little room for an increase in right hand selection.

A second possibility is that the left PPC stimulation led to a reduction in right hand preference by perturbing neural circuits involved in setting hand preference before decision and response processes were initiated. To investigate this possibility, we examined the relationship between the baseline hand preference bias in the no-TMS condition and the effect of left-PPC stimulation. Contrary to the hypothesis that left PPC TMS affected handedness, we found no correlation between these two measures (Fig. S2).

A third possibility is that the left PPC is involved in planning reaches for both hands (50–52), whereas the right PPC is only involved in planning reaches for the left hand. The left PPC has been implicated in "motor attention" (52–55), praxis (48, 50, 56), and the selection of responses, irrespective of the hand used (51). Furthermore, lesions to the left PPC lead to more pronounced deficits in selection and preparation of limb movements than lesions to the right PPC (55, 57). Given such an asymmetry, TMS of the right PPC might not lead to observable changes in hand preference because the left PPC may be able to compensate when activity in the right PPC is disrupted. This account of the asymmetry is analogous to the attention-competition hypothesis for the effects of parietal lobe lesions in unilateral neglect, where it has been proposed that the right parietal lobe is involved in directing attention to both visual fields, whereas the left parietal lobe is limited to directing attention to the right visual field (58).

We also considered the possibility that the TMS effects reflect a disruption of attentional processes rather than hand selection per se. Although parietal TMS has been found to produce transient impairment in processing visual targets (35), an attention-based account is not consistent with the present RT results. We found no interaction between the hemisphere of stimulation and visual hemifield of the target, arguing that TMS affected hand selection or reach planning rather than attentional or lower level perceptual processes. We recognize that one has to be careful in interpreting null results. Nonetheless, our interpretation is also consistent with evidence from single-cell recordings in monkeys showing that PPC activity was more predictive of movement intention than the locus of attention (9), from human neuroimaging showing that the PPC was strongly responsive to arbitrary stimulus-response associations but only weakly responsive to the perceptual properties of stimuli (5), and from TMS in humans showing that disruption of PPC function had an effect on motor but not visual coordinates for reach planning (59, but also see ref. 60 for an alternative view).

In summary, the current results provide strong evidence that decisions of hand choice involve a process that resolves a competition arising from the parallel engagement of action plans for both hands. Serial models in which hand choice is made at a higher cognitive level without activation of action plans for both hands might have predicted an increase in RT with TMS but cannot account for the shift in hand use. Rather, the results indicate that motor planning is initiated before response selection is made (17). Indeed, the emergence of decisions and actions can be viewed as a dynamic process in which many possible motor responses are competing at any one time, with the accumulation of evidence in favor of each candidate response continuously changing as a product of the interaction of a personal history and the current context (5, 17, 19, 20).

In terms of the neural instantiation of these processes, the present results provide further evidence for the role of the PPC in the representation of response specific decision variables (2, 3). Previous studies have focused on spatial decisions related to the selection of a target (6, 61). Here we are unique in providing causal evidence that the PPC is also involved in a fundamental decision related to hand choice, even when the stimulus itself does not directly specify that information (8). Although it is likely that a broad network of cortical and subcortical areas are involved in different aspects of decision-making (4, 7), the present results highlight the critical role that the PPC has in transforming sensory information into free choices of action (7, 8).

Materials and Methods

Participants. Participants were all right-handed and experiment-naive (experiment 1: n = 13, six women, mean age = 19.8 y, range = 18–21 y; experiment 2: n = 10, two women, mean age = 25 y, range: 21–33 y; control experiment: n = 10, six women, mean age = 21.7, range: 20–24 y). The protocol was approved by the University of California Berkeley Institutional Review Board. Participants provided written informed consent at the start of the test session.

Procedures. *Experiment 1.* Participants sat with their hands positioned on a table surface while a 3D motion-tracking system monitored the position of their hands. Feedback in the form of two white dots was projected on a horizontal screen and indicated the current position of each hand (Fig. 1*A*). Three circles were always visible to participants. Two of these circles indicated the starting location for the hands. A "+" symbol was displayed within the third circle, indicating the visual fixation location. After the participants had maintained the starting position for a variable period, they were presented with one of three types of trials (Fig. 1*C*). On unimanual trials, a single target circle was presented in 1 of 10 possible locations. These locations were arranged in a semicircular array (Fig. 1*B*). The participant was instructed to reach as quickly as possible to the target location, using one hand. In addition to the unimanual reach trials, we also included two types of catch trials. On bimanual-catch trials, two target circles were presented and the participant had to reach to both targets simultaneously, one with each hand. These trials were included to ensure that participants remained ready to respond with both hands, reducing the likelihood that participants might adopt a strategy of always using the same hand. Participants responded accurately in 91% of the bimanual catch trials. For fixation-catch trials, the "+" in the center of the fixation circle changed to an "×." Participants were required to move both hands into the fixation circle on these trials. The fixation-catch trials were included to ensure that fixation was maintained at the start of each trial. We instructed participants that they were free to move their eyes once a target had been displayed. Participants responded accurately in 95.9% of the fixation-catch trials.

Each participant completed 14 blocks of 48 trials each (6 CHOICE, 4 RIGHT-ONLY, and 4 LEFT-ONLY), with the order pseudorandomly assigned. Each block included four unimanual trials for each of the 10 target locations. CHOICE blocks also had four fixation-catch trials and four bimanual-catch trials. RIGHT-ONLY and LEFT-ONLY blocks had eight fixation-catch trials and no bimanual-catch trials.

Experiment 2. At the start of the testing session, the target scalp locations for TMS of the left hemisphere and right hemisphere PPC were established on an individual basis. We used anatomical MRI and a frameless stereotaxic localization system to identify the scalp location over the caudal part of the IPS, just anterior to the parieto-occipital sulcus (Fig. 4). For setting the stimulation level, we used a criterion based on the motor threshold for the left hand at rest. The motor threshold value was set to the stimulation level that elicited visible movements of the fingers in four of eight TMS pulses applied to the hand area in the primary motor cortex. TMS pulses were generated by a rapid stimulator configured with an air-cooled figure-eight 70-mm coil.

For the reaching part of the experiment, the procedures were similar to that of experiment 1, but only the CHOICE condition was tested. Each participant completed 12 test blocks of 72 trials each. A test block included six unimanual trials per target location, six bimanual-catch trials and six fixation-catch trials. Participants responded accurately in 94.9% of bimanual-catch trials and 99.1% of fixation-catch trials.

In the left-PPC and the right-PPC blocks, participants received a single TMS pulse at 120% of the motor threshold on every trial. The pulse was applied 100 ms after the onset of the reach target. The orientation of the coil was along the rostro-caudal axis, with the handle pointing caudally. In the no-TMS condition participants did not receive TMS. Block order was pseudorandomly determined such that each of the three conditions occurred once every three blocks.

We conducted a follow-up, control experiment in which the TMS was directed at a control site. For this experiment, we adopted a procedure used previously to target the primary somatosensory cortex (62, 63). The targeted location was determined on an individual basis by moving the TMS coil posterior from the scalp location found to produce maximal finger movements in each hemisphere. The posterior shift was repeated in 5-mm steps until TMS pulses at 120% of the motor threshold produced no visible finger movements and participants reported feeling no muscle twitches in response to the TMS pulses. The average shift was 28.5 mm (8.3 mm SD). The orientation of the coil was 45° relative to the midsagittal line. All of the other procedures in this control experiment were identical to that used with participants receiving PPC stimulation. Participants responded accurately in 93.7% of bimanual-catch trials and 99.4% of fixation-catch trials.

Analysis and statistics. To measure hand preference, we calculated for each condition the participants' probability of using the right and left hand for each target. By fitting a logistic regression curve to this psychometric function, we determined the PSE, the estimated location at which participants were equally likely to use the right or left hand (Fig. 2 and Fig. S3). To assess the effect of TMS on hand choice in experiment 2 and in the follow-up control experiment, we calculated the percent-change in ipsilateral hand use by calculating the difference in probability of ipsilateral hand use between the TMS condition of interest (left-PPC, right-PPC, left-CONTOL, or right-CONTROL) and the no-TMS condition, and then dividing this difference by the probability in the no-TMS condition. We also directly compared the left-PPC to right-PPC, and left-CONTROL to right-CONTROL stimulation conditions.

As a measure of response preparation, RT was defined as the time from the onset of the target to the time the cursor moved outside the starting circle. Median RT was determined for each condition (experiment 1: LEFT-ONLY, RIGHT-ONLY, CHOICE; experiment 2: left-PPC, right-PPC, no-TMS; control experiment: left-CONTROL, right-CONTROL, no-TMS). To assess the effect of hand choice on preparatory processes, we created two variables, one reflecting targets at the least ambiguous locations with respect to hand choice and one reflecting targets at the most ambiguous locations. For the former, we combined the data for the two extreme targets (the outermost right and left targets in the target array); for the latter, we combined the data for the two targets around the PSE. An additional analysis in experiment 1 combined the pooled data from the RIGHT-ONLY and LEFT-ONLY conditions to represent trials in which hand choice was predetermined to compare it to the CHOICE condition. Trials in which both hands moved, or in which none of the hands moved, were excluded from all analyses.

Dependent variables were analyzed using permutation tests. For all pairwise comparisons we performed one-tailed paired permutation tests based on all possible permutations of the condition labels (2^{13} for experiment 1 and 2^{10} for experiment 2 and for the control experiment). To look at the effect of target location and hand choice condition in experiment 1, we performed a 2 (target location: Extreme, PSE) by 2 (hand choice condition: PREDETERMINED, CHOICE) repeated-measures permutational ANOVA. To look at the effect of TMS condition by which visual hemifield the target was displayed on (experiment 2), we performed a 2 (visual hemifield: right, left) by 3 (TMS condition: left-PPC, right-PPC, no-TMS) repeated-measures permutational ANOVA (64). Permutational ANOVAs were based on 10,000 permutations of the data. We calculated bias corrected and accelerated bootstrap confidence intervals by creating a paired-sample bootstrap distribution of 10,000 resamples of the data (65).

A more detailed description of the materials and methods can be found in *SI Materials and Methods*.

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