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Sensory-motor mechanisms in human parietal cortex underlie arbitrary visual decisions

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The neural mechanism underlying simple perceptual decision-making in monkeys has been recently conceptualized as an integrative process in which sensory evidence supporting different response options accumulates gradually over time. For example, intraparietal neurons accumulate motion information in favor of a specific oculomotor choice over time. It is unclear, however, whether this mechanism generalizes to more complex decisions that are based on arbitrary stimulus-response associations. In a task requiring arbitrary association of visual stimuli (faces or places) with different actions (eye or hand-pointing movements), we found that activity of effector-specific regions in human posterior parietal cortex reflected the 'strength' of the sensory evidence in favor of the preferred response. These regions did not respond to sensory stimuli *per se* but integrated sensory evidence toward the decision outcome. We conclude that even arbitrary decisions can be mediated by sensory-motor mechanisms that are completely triggered by contextual stimulus-response associations.

Human decision-making is thought to involve higher-order task-independent cognitive processes, which are distinct from task-specific perceptual mechanisms that provide evidence in favor of a particular choice and from motor mechanisms that are responsible for producing the chosen action[1,2]. However, at least simple visual decisions in monkeys are mediated by neural mechanisms that are embedded in the sensory-motor apparatus. In critical experiments with monkeys trained to discriminate the direction of moving dots, oculomotor neurons in the lateral intraparietal area (LIP) increase their response in proportion to the level of sensory evidence in favor of a saccadic choice toward their receptive field[3,4].

It is currently unknown, however, whether the proposed mechanism also generalizes to human decisions, which are instead characterized by arbitrary stimulus-response associations that change over time according to contextual factors. To understand how sensory representations are converted into the behavioral outcome of arbitrary decisions, we trained human subjects to associate different visual stimuli (faces or places) with different actions (saccadic eye or hand-pointing movements). We systematically manipulated the level of noise that was added to the visual stimuli to study decision-making as a function of the quantity of sensory evidence available and to evaluate, especially for stimuli near the psychophysical threshold (that is, at 50% accuracy), decisions between competing response options in the absence of valid sensory evidence.

If arbitrary human visual decisions are made on the basis of mechanisms that are analogous to those identified in monkey studies[3,4], then activity in cortical regions responsible for the selection of the appropriate response should reflect the level of certainty of the decision. We studied a specific set of regions in human parietal and frontal cortex that carry motor signals that are specific for planning or executing either hand-pointing or saccadic eye movements, and we asked whether preparatory activity in these regions represented the level of sensory evidence in favor or against the motor choice for which they are selective. Critically, sensory evidence in our procedure was provided by visual stimuli (faces or places) that normally do not sensorially drive these regions but had been arbitrarily associated with a specific response in the context of the decision task. We found that two pointing-selective regions in medial parietal cortex, which do not respond to face or place stimuli *per se*, showed a pattern of activity that scaled with the strength of the sensory evidence in favor of a pointing response. A posterior intra-parietal region that was selective for saccades showed a more complex pattern, with a mixture of decision and attention signals related to perceptual difficulty.

RESULTS

We recorded blood oxygen level–dependent (BOLD) signal time series with functional magnetic resonance imaging (fMRI) during a visual decision task using an event-related fMRI design. In a typical trial (**Fig. 1a**), either a face or a place image was centrally presented with a peripheral visual target. Following a delay, subjects reported whether they had seen a face or a place by performing a saccade or a pointing movement, respectively, toward the remembered location of the visual target. We added a variable amount of noise to the face/place image on each trial to manipulate the amount of sensory evidence in favor of a saccadic/pointing decision. To match the level of sensory evidence across subjects, each subject performed a behavioral session in which

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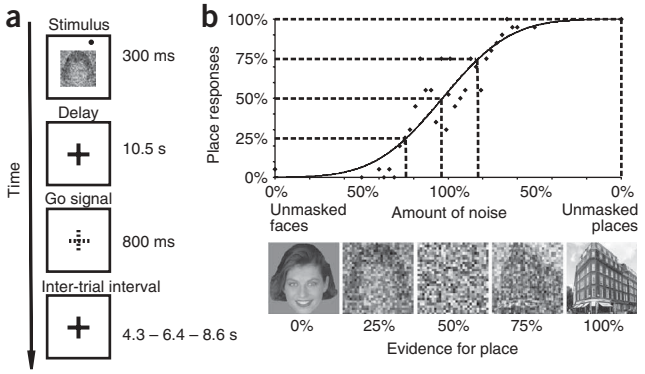

Figure 1 Decision task. (**a**) Procedure. A central image was presented to the subjects (a photograph of a face or a place with a variable amount of white noise superimposed) together with a peripheral target (a circle). After a delay, the fixation point changed color (go signal) and participants either moved their eyes (for faces) or pointed with their right index finger (for places) to the memorized target location and then immediately returned to the starting point. (**b**) Psychophysics and example of individual selection of evidence levels. The solid curve represents the best-fitting psychometric function for a representative subject, describing the probability of giving a place response as a function of the evidence level in the image. The scatter plot shows the raw data from which the estimate was computed. Bottom, examples of the five noise levels selected for this subject by interpolation of the psychometric function to yield 0%, 25%, 50%, 75% and 100% evidence for a pointing response.

images were categorized as either faces or places. For each subject, responses were fitted to a psychometric function[5,6], which was then interpolated so as to select stimuli categorized as places 0%, 25%, 50%, 75% and 100% of the time (**Fig. 1b**).

Action-selective and preparatory signals

Because we predicted that sensory evidence in favor of a given choice was represented in cortical regions that are responsible for the selection of the corresponding response, we conducted the main analysis on a specific set of pointing- and saccade-selective regions of interest (ROIs) in parietal and frontal cortex (**Fig. 2**). These regions were individually localized in each subject by recording a separate set of fMRI scans during blocks of memory-guided pointing or saccadic eye movements to visual targets.

We identified two pointing-selective ROIs in the precuneus, on the medial surface of the parietal lobe, which we labeled the anterior parietal reach region (aPRR; **Fig. 3**) and the posterior parietal reach region (pPRR; **Fig. 4**) for their relative locations on the basis of the localizer scans. On the lateral surface of the parietal lobe, we identified a saccade-selective ROI in the medial bank of the posterior intraparietal sulcus (pIPS; **Fig. 5**). In frontal cortex, we identified three action-selective ROIs (**Fig. 6**). Two were pointing-selective: a left central sulcus region spanning sensory-motor cortex (SMC) and a region in the dorsal aspect of the precentral sulcus or frontal reach region (FRR, SMC; **Fig. 6a**). The third one was saccade-selective and was located at the intersection of the precentral sulcus with the posterior end of the superior frontal sulcus (frontal eye fields, FEF; **Fig. 6b**). Because of their location and results from previous functional imaging studies, pointing-selective regions in posterior parietal cortex may be homologs of macaque areas medial intraparietal area and V6A, which are part of the monkey PRR[7–10], and saccade-selective regions pIPS and FEF may be homologs of macaque areas LIP and FEF, respectively[10–14].

For each ROI, we averaged the BOLD signal time series for each condition of the decision task across trials in each individual and then averaged the time series across subjects (see Methods). Inspection of the time series showed a first peak corresponding to the presentation of the visual stimulus (face, place) and the associated decision, and a second peak corresponding to the executed movement.

First, we determined whether activity during the first peak was significantly modulated by the planned response. Under conditions in which movement selection was easier (that is, when the place/face stimulus was clearly visible, 100% level of evidence), both aPRR and pPRR responded more strongly when subjects planned a pointing movement than an eye movement (response effector (pointing, saccade) by time (time points 1–6) interaction; aPRR: $F_{5,55} = 8.35$, $P < 0.001$; pPRR: $F_{5,45} = 4.37$, $P = 0.002$; **Figs. 3b** and **4b**). Saccade-selective signals in the pIPS were weaker and emerged toward the end of the delay period (response effector main effect: $F_{1,9} = 3.59$, $P = 0.09$; *post hoc* time point 5, $P = 0.001$; time point 6,

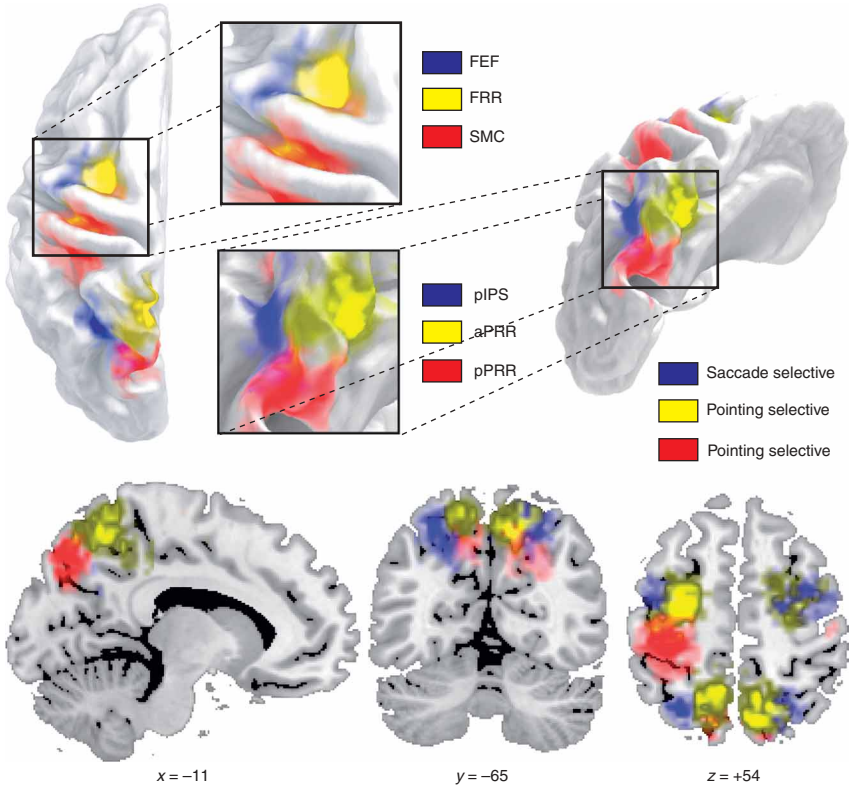

Figure 2 Pointing- and saccade-selective regions in posterior parietal and frontal cortex. Conjunction of individual ROIs from localizer scan for FEF, FRR, SMC, pIPS, aPRR and pPRR shown on a dorsal (on the left) and dorso-medial (on the right) view of the inflated surface of the left hemisphere of the PALS atlas[42] and coronal, sagittal and transversal slices of the Colin brain[43].

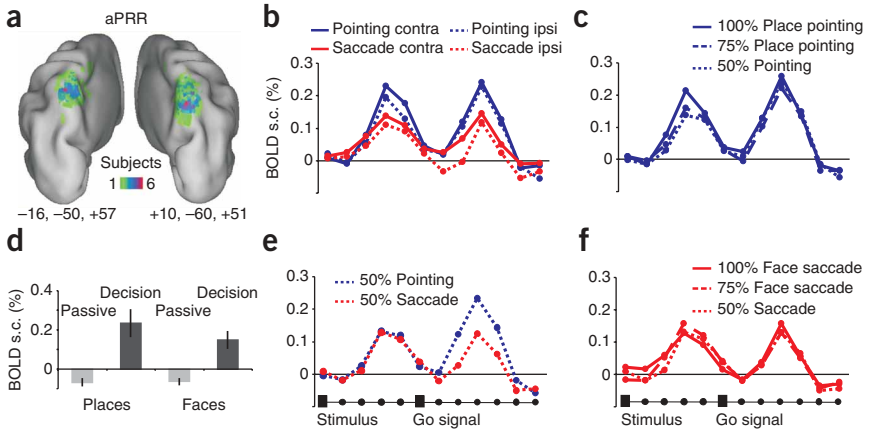

Figure 3 aPRR. (**a**) Left and right anatomical location of aPRR. Color scale indicates overlap of individual ROIs selected on the basis of the localizer scans displayed on the inflated surface of the PALS atlas[42]. (**b**) BOLD signal time series for pointing or saccadic eye movements to contralateral or ipsilateral targets. (**c**) Time series for trials in which subjects selected a pointing movement to place stimuli with different levels of 'positive' sensory evidence (100%, 75% or 50%). (**d**) Percent signal change to face and place stimuli during passive stimulation before training on the decision task (passive) and during the decision task (decision). Error bars represent the s.e.m. (**e**) Time series for trials in which stimuli provided no useful information (50% evidence) and subjects selected either pointing or eye movements. (**f**) Time series for trials in which subjects selected an eye movement to face stimuli at different levels of sensory evidence (100%, 75% or 50%).

$P = 0.004$; **Fig. 5b**). Robust effector-selective intentional signals in posterior parietal cortex contrasted with relatively weak effector-selective preparatory activity in frontal regions. The SMC region showed only weak pointing selectivity during the delay, whereas we observed no selectivity for pointing in the frontal FRR region (**Fig. 6c**) or for saccades in FEF (**Fig. 6d**). However, all of these regions showed robust effector selectivity during the response phase of the trial.

Accumulation of sensory evidence in parietal cortex

We next considered whether the level of activity covaried with the level of sensory evidence. Inspection of the BOLD signal time series on trials in which subjects selected a pointing response showed that the magnitude of the first peak varied with the strength of the sensory evidence in both aPRR and pPRR (100% > 75% > 50% evidence; evidence by time interaction; aPRR: $F_{10,110} = 2.71$, $P = 0.005$; pPRR: $F_{10,90} = 3.04$, $P = 0.002$; **Figs. 3c** and **4c**). In the pIPS region, modulation by the sensory evidence emerged relatively late in the course of the delay, similar to what we observed for saccade selectivity (evidence by time interaction: $F_{12,108} = 2.08$, $P = 0.024$; **Fig. 5c**). Notably, this modulation was not evident during the second peak for the movement execution in any of the three regions. This is consistent with the idea that decisions were made early on after stimulus presentation and that the quality of sensory information does not affect the execution of a movement once a threshold for decision is reached.

Bolstering the notion of an accumulator mechanism that integrates sensory evidence into a premotor plan, we looked for the presence of modulation by 'negative' sensory evidence (that is, favoring the nonpreferred response). At least in aPRR (**Fig. 3f**) and pPRR (**Fig. 4f**), the weakest peak response was observed when 100% face stimuli, strongly linked to a saccadic eye movement, were presented. This qualitative observation was validated by an ANOVA comparing the level of sensory evidence for the preferred effector over time points. For example, in pointing-selective regions, we compared responses to 100% place, 75% place (25% face), 25% place (75% face) and 0% place (100% face) stimuli. We observed a significant interaction of level of sensory evidence by time (aPRR: $F_{15,165} = 3.51$, $P = 0.001$; pPRR: $F_{15,135} = 1.95$, $P = 0.023$), which was significant at the peak of the response (time point 4) (*post hoc t* tests, aPRR: 100% place > 75% place, $P < 0.001$; > 25% place, $P < 0.001$; > 0% place, $P < 0.001$; pPRR: 100% place > 75% place, $P = 0.011$; > 25% place, $P = 0.042$; > 0% place, $P < 0.001$). In the saccadic region pIPS (**Fig. 5f**), we also found an interaction of level of sensory evidence by time ($F_{15,135} = 1.88$, $P = 0.030$), which was significant at the end of the delay (time point 6), similar to what we found for saccade selectivity and positive sensory evidence (*post hoc t* tests, 100% face > 25% face, $P = 0.004$; > 0% face, $P < 0.001$).

These results indicate that all of the effector-specific regions in posterior parietal cortex are modulated by both positive and negative sensory evidence. Overall, these findings strongly suggest that arbitrary decisions rely on an accumulator mechanism that integrates sensory evidence toward a motor response. To rule out the possibility that this modulation by sensory evidence reflected a low-level perceptual effect, such as a stronger response to clearly visible stimuli (100% face or place) than to noisy ones (50% face/place), or a differential specificity of pointing or saccade regions to these stimulus categories, we compared sensory responses to face and place stimuli before and after subjects were exposed to the decision task.

We ran blocks of trials involving the passive presentation of face and place stimuli before the subjects were ever exposed to the visual decision task. Before training, the passive sensory responses to place or face images were generally weak in posterior parietal cortex. However, during the decision task (that is, after training), responses became strong and selective. This difference, at least in aPRR, cannot be

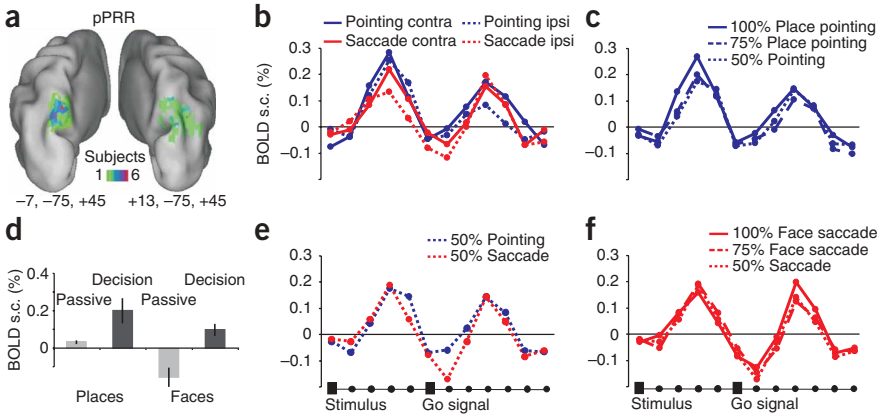

Figure 4 pPRR. **a**–**f**. Data is presented as in **Figure 3**.

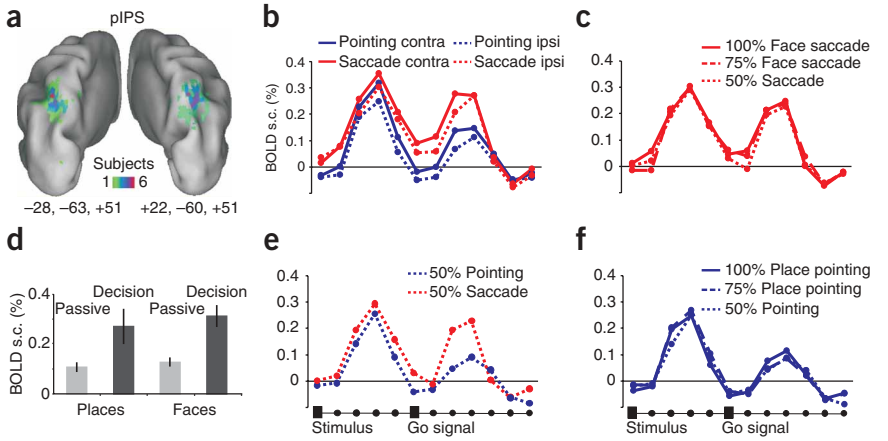

Figure 5 pIPS region. **a**–**f**. Data is presented as in **Figure 3**.

accounted for by variation in arousal or attention, as the activation became not only stronger but also more selective, for the stimulus category associated with the preferred response (experiment (passive, decision) by stimulus (face, place) interaction: $F_{1,10} = 8.13$, $P = 0.017$; **Fig. 3d**). In pPRR, we observed the same trend, although it was not significant ($F_{1,8} = 0.96$, $P = 0.35$; **Fig. 4d**), whereas the response to both types of stimuli increased during the decision task in the pIPS region (**Fig. 5d**). In summary, the response in these regions is not the result of low-level sensory factors but is probably the product of learning the arbitrary visuo-motor association.

Spatial and decision signals in parietal cortex

Activity in posterior parietal cortex was not only modulated by the strength of the sensory evidence but also by the direction of movement or spatial location of the target. In fact, the pointing aPRR (**Fig. 2b**), pointing pPRR (**Fig. 3b**) and saccadic pIPS regions (**Fig. 4b**) showed stronger responses for targets/movements toward the contralateral visual space (visual field by time interaction, aPRR: $F_{5,55} = 5.69$, $P < 0.001$; pIPS: $F_{5,45} = 5.21$, $P < 0.001$; visual field main effect, pPRR: $F_{1,9} = 12.17$, $P = 0.006$). This spatial selectivity was independent of motor planning signals, as indicated by the lack of a significant interaction of response effector by visual field (response effector by visual field by time, aPRR: $F_{5,55} = 0.11$, $P = 0.987$; pPRR: $F_{5,45} = 1.64$, $P = 0.167$; pIPS: $F_{5,45} = 0.32$, $P = 0.894$).

We also analyzed the response in aPRR, pPRR and pIPS regions when the stimuli provided no useful information (50% evidence) as a function of whether subjects selected pointing or eye movements. This is an important test of whether these regions actually code for the motor decision independently of the quality of sensory information. Notably, although aPRR was not modulated by motor choice (**Fig. 3e**), preparatory signals in both pPRR (**Fig. 4e**) and pIPS regions (**Fig. 5e**) predicted the subject's decision. In pPRR, the early part of the time course (including the peak) did not distinguish between pointing and eye movements, consistent with an ongoing competition between the two response outcomes; however, a differentiation emerged later in the course of the delay (time point 5), which is consistent with a relative delay in reaching the decision when the sensory evidence was poor (response effector by time interaction, pPRR: $F_{5,45} = 2.73$, $P = 0.031$; *post hoc t* tests on time point 5, $P = 0.001$). In the pIPS region, the decision to make a saccade modulated activity after the peak toward the end of the delay period (response effector main effect: $F_{1,9} = 6.35$, $P = 0.03$), consistent with the late emergence of other selective signals during the delay.

In summary, although all regions were sensitive to the effector, the quality of sensory information and the spatial location of the target, pPRR and pIPS were also modulated by the actual 'choice' to move.

Sensory evidence and decision in frontal cortex

In contrast with the parietal regions, the FRR (**Fig. 6e**) and the FEF saccade-selective region (**Fig. 6f**) were not modulated by the level of sensory evidence during the decision delay (evidence by time interaction, FRR: $F_{10,110} = 0.75$, $P = 0.667$; FEF: $F_{10,80} = 0.59$, $P = 0.812$). Even though these regions were classified as pointing- and saccade-selective on the basis of the localizer scans and manifested effector-specific activity during execution (**Fig. 6c**,**d**), they did not show strong selective planning activity and did not predict the outcome of the decision when the stimuli were ambiguous.

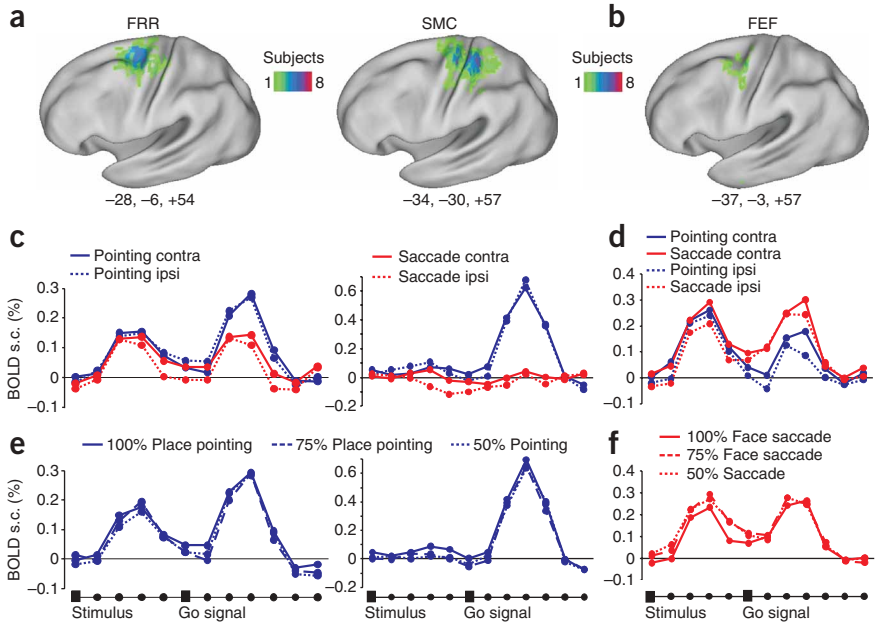

Figure 6 FRR, SMC and FEF. (**a**,**b**) Left hemisphere anatomical location of FRR, SMC (pointing) and FEF (saccade) regions. (**c**,**d**) BOLD signal time series for pointing or eye movements to contralateral or ipsilateral targets. (**e**) Time series for trials in which subjects selected a pointing movement to place stimuli at different levels of sensory evidence (100%, 75% or 50%). (**f**) Time series for trials in which subjects selected an eye movement to face stimuli at different levels of sensory evidence (100%, 75% or 50%).

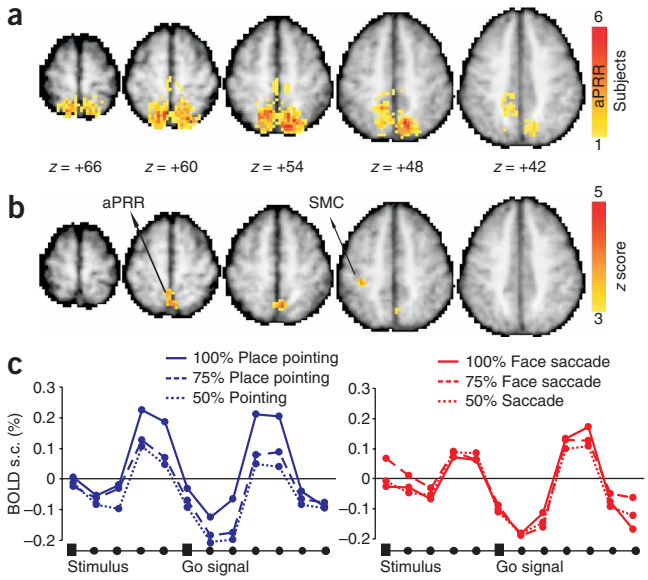

Figure 7 Whole brain analysis: sensory evidence and effector selectivity. (**a**) Color scale indicates overlap of individual aPRR ROIs on the basis of localizer scan mapped onto transverse slices of the Colin brain[43]. (**b**) Multiple-comparison corrected *z* map of the interaction of response effector by sensory evidence by time. (**c**) BOLD signal time series from aPRR region in b for trials in which subjects selected either a pointing or an eye movement to stimuli at different levels of sensory evidence.

These negative results during the delay, vis-à-vis the selectivity of responses during execution and the pattern in posterior parietal cortex, suggest that the premotor regions FRR and FEF were more involved in late motor selection and/or execution than in the transformation of sensory information into motor plans. In SMC, however, there was some evidence for accumulation of sensory evidence and specificity for arm motor planning (**Fig. 6c,e**). The response during the decision delay was stronger for 100% than for 75% or 50% place stimuli (sensory evidence main effect, $F_{2,22} = 7.17$, $P = 0.003$). There was also stronger delay activity for pointing than for saccades (response effector main effect, $F_{1,11} = 8.22$, $P = 0.015$).

Sensory evidence outside action-selective regions

Although our results strongly suggest that posterior parietal cortex is predominantly influenced by the accumulation of sensory evidence and ensuing motor decisions, two important questions remain unanswered by the main ROI analysis. First, are there other effector-specific regions that also show decision signals? Second, are there any brain regions that accumulate sensory evidence independently of motor plan or response type? In other words, is there evidence for a neural correlate of a general decision-making module? Two recent fMRI studies report that activity in left superior dorso-lateral prefrontal cortex is compatible with such a mechanism[15,16].

We investigated these two questions by running a voxel-wise ANOVA on the whole brain, with response effector, sensory evidence and time as factors. An interaction of response effector by sensory evidence by time would identify voxels in the brain that are sensitive to both response selection and sensory evidence. Conversely, a significant interaction of sensory evidence by time would be indicative of voxels that are modulated by sensory evidence independently of the specific motor response and may thus represent a more general decision-making mechanism.

Consistent with the ROI analysis, we found an interaction of response effector by sensory evidence by time in a medial parietal region in the precuneus that completely overlapped with aPRR (**Fig. 7a,b**). This area responded more strongly to pointing than to saccadic movements during the decision delay and showed a modulation by sensory evidence in the expected direction (100% > 75% > 50% evidence; **Fig. 7c**). The only other significant region was localized in the left central sulcus and it was also entirely included in the SMC region (multiple comparison corrected *z* map significant at the cluster level of $P = 0.05$). These analyses strongly and independently confirm the specificity of posterior parietal cortex and SMC in the accumulation of sensory-motor evidence.

Next, we considered whether any region in the brain revealed an effect of sensory evidence irrespective of response effector. Several anterior regions, including ventral (left: –35, +43, +10; right: +43, +26, +24) and lateral prefrontal cortex (left: –36, –5, +25; right: +36, 0, +36), bilateral insula (left: –30, +18, +6; right: +36, +15, +2), pre-supplementary motor area (pre-SMA 0, +14, +43), and anterior cingulate (–4, +46, +1), showed a significant main effect of sensory evidence (**Fig. 8a–c**). Time series inspection revealed stronger activation for more difficult stimuli (50% and 75% evidence) than for easier stimuli (100% evidence). Notably, this effect was independent of the response effector (saccade or pointing). This pattern of results is consistent with a role for these prefrontal regions in perceptual analysis or allocation of attention resources but not in accumulation of sensory evidence or decision-making.

We also observed a main effect of sensory evidence bilaterally in the IPS (left: –29, –63, +47; right: +30,–61, +46), which overlapped with the saccadic region pIPS and similarly displayed saccadic-selective motor activity (**Fig. 8d**). Therefore, this part of posterior parietal cortex contains a mixture of perceptual-attention, sensory evidence and motor-decision signals.

Finally, several other brain regions showed a deactivation that was independent of stimuli and responses. The deactivation increased with stimulus difficulty: that is, stronger for 50% and 75% than for 100% evidence. These regions included posterior cingulate, ventro-medial prefrontal cortex and angular gyrus, the main nodes of the so-called 'default' system[17,18], a functional network that is consistently deactivated during goal-directed behavior when compared with rest (see

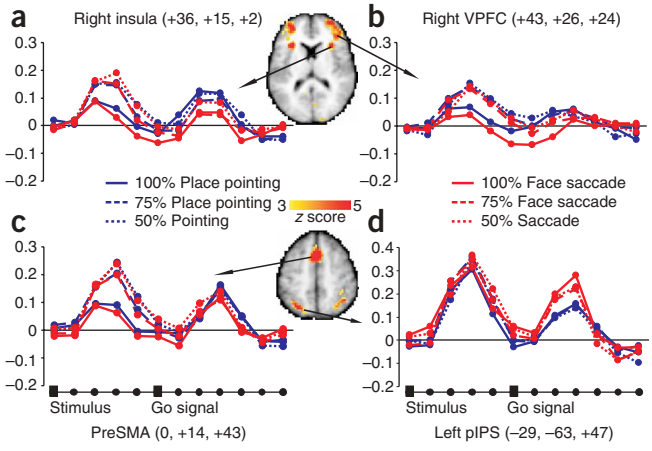

Figure 8 Whole brain analysis: sensory evidence. (**a–d**) Multiple-comparison corrected *z* map of the main effect of sensory evidence is superimposed on selected transverse slices of the Colin brain[43]. BOLD signal time series for pointing and eye movements as function of sensory evidence. preSMA, pre-supplementary motor area; VPFC, ventro-medial prefrontal cortex.

Supplementary Fig. 1 online for the location and time series of these regions in relation to the topography of the default network). The negative modulation of these regions as function of task difficulty is compatible with previously reported load- or attention-dependent modulations of the default network[19,20] but not with a role of these regions in the accumulation of sensory evidence. Notably, the region in dorso-lateral prefrontal cortex that has been proposed to be a general decision-making module[16] falls in the borders of the default network and, not surprisingly, showed a signal deactivation (see **Supplementary Fig. 1**). In conclusion, we found no prefrontal region with a positive modulation related to sensory evidence independent of the motor response.

DISCUSSION

Sensory evidence and decision signals in parietal cortex

The main finding of our study was that arbitrary visual decisions involving the association of a stimulus to a response did not involve a general decision-making module but rather depended on specific sensory-motor mechanisms that accumulate sensory information and plan motor actions. Several regions in human posterior parietal cortex that are specific for planning and executing either pointing or saccadic eye movements responded more strongly to stimuli that provided more sensory evidence toward a motor decision and that were linked to the preferred response in the context of the decision task.

The modulation by sensory evidence cannot be explained by a difference in the sensory response to highly visible (100% evidence) versus noisy stimuli (50% evidence) because these regions did not respond to highly visible place or face stimuli before they became relevant as part of the decision procedure. Rather, parietal cortex became strongly responsive to the relevant stimulus category (face or place) in the context of the decision task. Although higher arousal or attention may partly account for an increment in the sensory drive of these regions, the enhancement was specific for the stimulus category (places) associated with the preferred movement (pointing), at least in the region aPRR. Higher responsiveness to task-relevant stimuli is consistent with reports of neurons in parietal cortex flexibly coding stimulus features instructing a selective task set[21–23].

Additional support for the idea that parietal cortex functions as an accumulator of sensory information is the modulation by both positive (that is, related to the preferred response) and 'negative' sensory evidence (that is, related to the nonpreferred response) (for example, saccade responses to face stimuli in a pointing region). In all three parietal regions (aPRR, pPRR and pIPS), the response scaled with evidence for both preferred and nonpreferred responses (for example, 100% place, 75% place, 25% place (75% face) and 0% place (100% face) in pointing-selective aPRR and pPRR). This control is important because it argues against a 'premotor' interpretation. A highly visible (high evidence) relevant stimulus leads to a quicker decision and thus potentially leads to an earlier and stronger build-up of premotor activity for the preferred movement. Conversely, a noisy stimulus (low evidence) leads to a delayed decision and possibly to a delayed and weaker motor build up. A premotor interpretation, however, predicts no modulation by negative evidence linked to the nonpreferred response. In contrast, we found that parietal cortex activity scaled as function of both positive and negative evidence, which is more consistent with a sensory mechanism that weights the available sensory information[3,4].

Parietal cortex contains not only sensory evidence signals but also motor signals related to the decision. This conclusion is based on three observations. First, these parietal regions were selected on the basis of their specificity for motor effectors in a localizer task that combined planning and execution, and, during the decision task, all three of the regions showed effector-specific planning activity. A functional subdivision of posterior parietal cortex in action-specific regions (eye, face and arm) is consistent in humans and monkeys. The location of the pointing-selective regions aPRR and pPRR, extending from the precuneus to the superior parietal lobule, matches the localization of pointing-selective activity in other neuroimaging studies[7,8], as well as the relative position of putatively homologous reaching-specific regions in the macaque monkey (PRR, medial intraparietal area and area V6A)[24]. Similarly, the location of the saccade-selective region pIPS, in the posterior aspect and medial bank of the intraparietal sulcus, is consistent with the localization of a topographically selective region that is responsive to eye movements and spatial attention in humans[7,11,25–27]. This region shows, consistent with previous work, weaker saccade-specific preparatory signals[7] but strong selectivity during execution. This region represents the putative homolog of macaque LIP, which also show similar response properties[10,12].

Second, two out of three regions (pPRR and pIPS) responded more strongly when subjects selected the preferred response under conditions in which the stimulus did not provide any useful information (50% sensory evidence). Therefore, activity in these regions predicts a motor decision independently of any sensory evidence. This is consistent with recent reports of monkey's PRR neurons responding to spontaneous choice of arm movements in the absence of instructing cues[28].

Third, these regions were spatially selective in relation to the target location or movement direction; that is, the response during the decision delay was stronger for contralateral than for ipsilateral targets/movements. A spatially selective response underlies either selection of the target stimulus or planning of movement direction. Notably, effector and spatially selective signals were independent and additively contributed to the response in these regions. This is consistent with results from both the PRR and LIP regions in the monkey, in which spatial and effector-specific signals are also largely independent from one another[29,30].

In summary, the combined functional properties of our posterior parietal regions strongly indicate that they contain the right mixture of signals (sensory evidence, motor and spatial) for implementing a simple decision-making mechanism on the basis of the continuous transformation of sensory information into motor decisions. In this case, the association between stimuli and responses was entirely arbitrary and was not tuned to the sensory properties of an area. This result generalizes a basic mechanism that was previously identified in macaques during simpler perceptual decisions[3,4] to more complex human decisions. However, the limited spatial resolution of fMRI does not allow us to distinguish whether these signals converge on the same neuronal population or whether they are distributed over different neuronal types or layers in the same region.

Parietal versus frontal cortex

In contrast with the strong decision-related signals in posterior parietal cortex, we found relatively weak evidence for accumulation of sensory evidence in frontal cortex. The pointing-selective FRR and the saccade-selective FEF region in premotor cortex were not modulated by either sensory evidence levels or decision outcome. The SMC showed weak effects of sensory evidence and motor planning but no decision outcome or spatially selective modulation. Furthermore, in a voxel-wise analysis to examine the interaction of sensory evidence and response effector, we still found a significant modulation (multiple comparison corrected z map significant at the cluster level of $P = 0.05$) of the pointing-selective aPRR in posterior parietal cortex and of the primary SMC but no effect in premotor or prefrontal cortex. This

negative finding must be weighed against single-unit evidence of sensory accumulation in dorsolateral prefrontal cortex[31] and the limited spatial resolution of fMRI in detecting individual neuronal populations in the same area.

In contrast, prefrontal regions including ventral and dorsolateral cortex, anterior insula, and anterior cingulate showed strong modulation by sensory information independent of effector. However, this effect was a result of stronger responses for difficult (for example, 50% evidence) than for easy (for example, 100% evidence) stimuli, which can be attributed to either perceptual difficulty or attention load but not to sensory evidence accumulation.

In summary, within the resolution of the fMRI methods that were used in this study, we can conclude that sensory-motor decision mechanisms seem to be specific to posterior parietal cortex. Furthermore, the modulation of preparatory activity in SMC by sensory evidence is consistent with continuous flow models of decision-making in which sensory evidence continuously flows from sensory to motor regions of the brain[32].

Sensory-motor versus general decision-making mechanisms

The fact that decision signals were localized in effector-specific regions, and that no region in the brain showed a positive modulation by level of sensory evidence independent of response, argues against the idea of a general abstract decision-making mechanism postulated in traditional psychological models[1].

A previous study[16] reported signals that scaled with the level of sensory evidence independently of motor responses in a left superior prefrontal region. Subjects performed a motion-discrimination task on displays containing different levels of coherent motion, similar to the original monkey experiments[3,4], and reported their decision using either an eye movement or a key press. The superior prefrontal region showed a stronger response to high than to low evidence stimuli and no specificity for the type of movement. The positive modulation by sensory evidence and the independence from motor plans were thought to support "the development of a more general decision-making module to accommodate the broader range and greater flexibility of human decisions[2]." This hypothesis conflicts with current evidence in nonhuman primates that perceptual decisions are closely tied to motor plans[3,4,31]. With the limitation of comparing responses across studies, we found that this prefrontal region is part of a more distributed network including lateral parietal cortex, posterior cingulate-precuneus and ventro-medial prefrontal cortex. This network corresponds to the so-called 'default' network[17,18], which is commonly deactivated during goal-directed behavior and suppressed during difficult perceptual or attentional demanding tasks[19,20]. As the deactivation is more profound for difficult (or low evidence) than for easier (or high evidence) stimuli, a direct contrast between these two conditions (as in ref. 16) may yield an apparent positive modulation by sensory evidence.

Conclusions

To the best of our knowledge, this is the first report to show that human posterior parietal cortex contains a sensory-motor mechanism for arbitrary visual decisions. Activity in posterior parietal cortex, specific for planning effector-specific movements, was modulated at the moment in which decisions were being formed by the level of sensory evidence, the position of the target and the outcome of the decision in the absence of helpful sensory information. These signals represent the neural correlate of a mechanism, completely trained by the experimental association, by which sensory evidence accumulates toward the behavioral outcome of an arbitrary decision. Moreover, in our hands, visual decisions in human subjects do not necessarily involve high-level representations independent of sensory-motor systems[2,16]. Rather, decision processes seem to be embodied in the direct transformations between relevant sensory and motor representations, with premotor circuitries weighting sensory evidence toward learned behavioral choices, consistent with an 'intentional architecture' of information flow[33]. More generally, these findings support the emerging idea of 'embodied cognition'[34], in which abstract cognitive functions do not depend on specialized modules but are built on simpler sensory-motor processing mechanisms. More simply said, "to see and decide is, in effect, to plan a motor response[35]."

METHODS

Subjects. We obtained written informed consent from the 12 healthy right-handed volunteers (8 females, mean age 24.2) who participated in the study. The experimental protocol was approved by the G. D'Annunzio University of Chieti's institutional ethics committee. Each participant completed a psychophysical calibration session (performed inside the magnetic resonance scanner to ensure stable stimulation conditions) for individual selection of levels of sensory evidence to be used in the decision task, an fMRI session of two localizer scans to localize effector-specific regions and two passive view scans to measure passive sensory responses to face and place stimuli in these same regions, a 1-h training session on the decision task to learn the stimulus-response association, and at least two fMRI sessions to perform the decision task.

Localizer and passive view scans. During each localizer scan, participants alternated eight blocks of delayed pointing movements, saccadic eye movements and fixation every 16 s. During each passive view scan, participants viewed eight alternating blocks (16 s) of unmasked faces and places presented for 300 ms every 500 ms, interleaved with fixation periods of 15 s on average.

Psychophysical calibration. During the psychophysical calibration session (**Fig. 1b**), a face/place image appeared centrally for 300 ms every 2 s, with a variable amount of white noise superimposed, in squares of 8 × 8 pixels. Face/place images were 240- × 240-pixel gray-scale digitized photographs selected from a larger set developed by N. Cohen (University of Illinois) and used in previous experiments[36–38]. Subjects responded by pressing one key for faces and one key for places. We randomly presented 20 trials for each of 35 equally spaced noise levels, forming a continuous range from unmasked faces through pure noise to unmasked places. A probit analysis of binomial responses based on maximum likelihood estimation[5,6] provided the threshold and slope of the psychometric function describing the probability of giving a place response as a function of the evidence level in the image. Interpolation of the individual psychometric function allowed us to select five noise levels for each individual, yielding 0%, 25%, 50%, 75% and 100% place responses.

Decision task. The decision task (**Fig. 1a**) included 20 scans of 24 trials each. A face/place image (at one of the five noise levels selected during calibration) was presented along with a peripheral visual target, a filled white circle (0.9-deg diameter) appearing in one of eight radial locations (1/8, 3/8, 5/8, 7/8, 9/8, 11/8, 13/8 or 15/8 π) at 4 deg eccentricity. After a delay, subjects reported whether they had seen a face or a place by performing an eye or a pointing movement, respectively, toward the remembered position of the peripheral target.

Data analysis. Functional images were analyzed on a voxel by voxel basis according to the general linear model. ROIs were identified from single subject z maps of contrasts[39] from the localizer scans and used for independent time series analysis during the decision experiment. Hemodynamic responses in the decision experiment were estimated without any shape assumption at the voxel level using the general linear model[40] and averaged across all the voxels of each ROI to generate regional time series. Individual time points of each estimated hemodynamic response, either on the regional data or at the single voxel, were entered into group analyses conducted through random-effect ANOVAs adjusted for correlations across time points[41], in which the experimental factors, including sensory evidence, response effector and visual field, were crossed with the time factor. Separate ANOVAs were conducted on the delay

and execution phases of the decision task (six time points each). Additional details are given in the **Supplementary Methods** online.

Note: Supplementary information is available on the Nature Neuroscience website.

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AUTHOR CONTRIBUTIONS

A.T., G.G. and M.C. were involved in experimental design. A.T. was responsible for data acquisition and data analysis, and A.T., G.G., G.L.R. and M.C. were involved in data interpretation and writing the manuscript.

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