Decoupling motor plans from perceptual decisions to investigate whether and when decisions are embodied

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Sandrone S. Decoupling motor plans from perceptual decisions to investigate whether and when decisions are embodied. J Neurophysiol 112: 1603–1605, 2014. First published March 12, 2014; doi:10.1152/jn.00308.2013.—Decision making is a crucial part of our life: we sense information from the environment and perform our motor response. However, “whether” and “when” decisions are embodied still needs to be fully elucidated. Neuroimaging data obtained by the disentanglement of perceptual decision from motor preparation revealed an increase in connectivity between inferior frontal cortex and sensory regions, and the important role played by intraparietal sulcus in motor decisions. The results obtained as well as the new research questions prompted by this work are carefully discussed herein.

decision making; motor plans; perceptual decisions; embodied cognition

EVERY DAY, FROM THE MOMENT the alarm clock sounds (and we are of two minds about getting out of the bed or postponing for a couple of minutes) until night, when we choose whether to set it again or not, we make a huge number of decisions, with a plethora of deeply intermingled cognitive, emotional, motor, spatial, and temporal aspects. In a paper recently published in the Journal of Neuroscience, Filimon et al. (2013) addressed the challenging topic of decision making using event-related functional magnetic resonance imaging (fMRI) and a well-designed experimental strategy. They disentangled motor preparation from perceptual decision making to investigate whether the sensorimotor system implements perceptual choices.

Previous research on this topic had been confounded by motor planning due to preassigned sensorimotor mappings (Shapiro 2011), leaving the question open of whether and when these decisions are embodied in brain circuits. Preceding neurophysiological studies on monkeys postulated the existence of a “decisional threshold” that can be reached by the accumulation of sensory information, with greater firing rates for perceptual decisions based on high sensory evidence, than those based on low evidence. However, increased firing patterns in frontal eye fields (FEF) and the lateral intraparietal area (LIP) (see for example Kim and Shadlen 1999) are misleading, since they could be correlated to motor plan preparation rather than to perceptual decisions or sensory integration. Evidence of the fact that prior expectation can modulate the interaction between sensory and prefrontal regions in the human brain has already been found (Rahnev et al. 2011), but the contribution of effector-specific sensorimotor regions to perceptual decisions is not so clear, given that effector-nonspecific areas also contribute to eye and hand movement planning. This scenario is further complicated by the fact that the human decisional threshold acts in multiple ways, e.g., with sustained activity vs. nonsustained activity modalities.

In light of that, Filimon et al. (2013) avoided a priori assumptions on the decisional threshold. From an epistemological point of view, this bottom-up experimental approach is probably the best solution when different theoretical frameworks are available and none of which can be identified as ultimately correct. They analyzed the increase in effective connectivity between sensory evidence areas and higher-level regions. In the process, they revealed target locations and the effector type to the experimental subjects only after the decision stage. After a training period, 19 people undertook a task in which they had to decide repeatedly whether grayscale noisy stimuli represented a face or a house, individually adjusted for each subject and presenting high or low levels of sensory evidence (i.e., with low or high levels of noise). All stimulus images had the same spatial frequency, contrast, and luminance. After a variable delay of up to 9 s, subjects were given a specific motor preparation instruction on how to indicate their decision. Starting from a fixation point, they were given an additional 1.5 s in which to respond either by saccading to the remembered target location (up, down, left, or right) or by pressing the corresponding button on a diamond-shaped response pad (hand trials). Eight possible motor plans were thus decoupled from perceptual decisions. During each motor preparation period, a star or a square, respectively representing a face or a house, appeared as a target at one of the aforementioned locations, and subjects responded without receiving any feedback.

The first finding of the experiment was that the subjects recognized faces and houses with high levels of accuracy, and even more so for increased sensory evidence, as witnessed by behavioral analysis and cerebral activations for presented stimuli. Faces activated face-dominant regions in occipital and ventral temporal cortices significantly more than did houses, which in turn mainly activated the parahippocampal gyrus, thus confirming previous reports (Kanwisher and Yovel 2006). However, the variability among subjects on cerebral shape and size and individual differences in ear canals as well as in lateral ventricles produced different field distortion in ventral temporal cortex in each subject. Therefore, registration of individual run to a standard space was imprecise, and could to some extent smear out the activations in the fusiform and parahippocampal gyri. Because of that, regions of interest were se-
lected at the single-subject level. Regardless of the sensory evidence level, all stimuli led to widespread BOLD activations that involved inter alia, the prefrontal cortex, FEF, the orbitofrontal region, intraparietal and parietal areas, the precuneus, the cingulate cortex, and subcortical structures. These activations probably reflected other mental processes and factors involved in this paradigm, such as attention, memory, difficulties, and other inter-individual differences.

The second finding was that psychophysiological interaction (PPI) analysis allowed the authors to identify the specific decision-making network and thus satisfy a requirement for increased effective connectivity with faces and house areas during the perceptual decisions. The combination of a PPI analysis with the comparison of the total amount of BOLD activation for high- vs. low-evidence conditions could be viewed as the fMRI equivalent of the postulated sensory evidence comparator process and the accumulation to threshold (see also Gold and Shadlen 2007). The authors hypothesized and empirically confirmed that, during the phase of sensory evidence integration, perceptual decision-making regions should systematically display higher connectivity with the absolute difference between time series from face- and house-dominant sensory regions over the perceptual decision period than during the rest of the trial, when motor planning is underway.

However, even with this approach, the aforementioned factors could still account for an increase in connectivity. The authors accordingly set three further stringent criteria: 1) that perceptual areas involved in sensory integration should also be modulated by the amount of sensory evidence available during the perceptual decision; 2) that said areas should show greater activation during the decision stage than the postdecision stage; and 3) that they should be activated above baseline. At the face/house decision stage, the effective connectivity increased substantially in several regions, but the inferior frontal sulcus (IFS) was the only region to meet the established criteria for sensory integration. The IFS responded to the sensory evidence independently of effector-specific motor preparation and reached a perceptual decision in the absence of a motor plan, without the need for the decision to be embodied. Motor plans cannot be formed in putative LIP. Although sensory evidence modulation over the perceptual decision in the parietal PPI areas was predictable (and possibly too weak to be detected with fMRI techniques), such modulation was recorded in prefrontal but not in parietal cortices, whose neurons enshrined a finer representation of very specific stimuli (Quiroga 2012). A reanalysis of the data on the basis of this specific point confirmed previous reports, therefore revealing a greater motor preparatory activity for oculomotor decisions with a greater putative LIP high > low modulation (Tosoni et al. 2008). This motor IFS region, interestingly also not overlapping with the PPI areas when a less stringent liberal threshold was applied, was indeed involved in motor and eye movement decisions between possible targets to be reached with a saccade, probably through its connectivity with middle temporal regions. The final observation of this study was that of higher IFS activation for low- than for high-evidence decisions. In contrast, LIP displayed a high > low pattern during motor decisions, which suggested for the first time that different regions and types of decisions have different neural signatures.

These results are striking, and some interesting and stimulating issues can be raised. We are still far from having ultimately mapped the LIP areas in monkeys and the equivalent ones in humans, and future investigations will have to fill this conceptual gap by properly addressing it from both structural (cytoarchitectonic) and functional (connectivity) perspectives. Also, modifying the paradigm so as to increase the number of the training trials would have made this study even more analogous to those performed in monkeys, allowing more meaningful comparison. Given that the experimental paradigm requires a saccadic movement, the authors correctly decided to use an eye tracker inside the fMRI. This tool is very useful when used to quantify the movements of the subjects before the final decision, to measure the point of gaze and the motion of an eye related to the head, and to analyze whether specific eye movements are linked to specific (i.e., correct vs. incorrect) decisional outcomes.

Thanks to the study by Filimon and colleagues (2013), we have learned that abstract decisions in the absence of sensorimotor mappings are not embodied, but that sensorimotor networks do contribute to motor decisions. Interestingly, some variants of the experimental strategy used by Filimon et al. could be really useful to gain further insights. The first of them could rely on the exploitation of visual lexical choice. Only tangentially discussed by the authors, a psycholinguistic version of their paradigm would enable modulation of the ambiguity inherent to the material presented, and it would facilitate a focus on the perceptual decision that involves the dichotomy between abstract and concrete (more embodied) stimuli. With these modifications, in fact, it would be possible to assess the contrast between eye, hand, and also mouth movements (Cappa and Pulvermüller 2012). Also, the use of multi-modal and cross-sensorial responses (e.g., audio-visual object responses) could expand the range of perceptual decisions considered here.

Crucial insights could also be gained by modifying the experimental design with the introduction of new factors as regressors. For example, the modulation of the response movement can be achieved by means of pointing or bimanual responses (Madlon-Kay et al. 2013) rather than of the less demanding button pressing. Conversely, exclusion of the high- and low-response targets could reduce the combinations of motor plans, and thus simplify the task.

Designing a well-controlled experiment where scientists can properly manipulate individual variables is a fundamental methodological issue, and Filimon and colleagues (2013) have elegantly done this. At the same time, however, we live in a dynamic and lively world where static stimuli are extremely rare. Therefore, one of the next challenging steps could be the use of a visual motion discrimination task instead of recognition, which could further reduce the gap between the experimental setting and our daily decision-making process. Moreover, displaying colored stimuli, in spite of a slight difficulty in individual adjustment, would make the task even more ecological.

There are many different kinds of decisions, and to obtain a complete picture we need to insert processes that are pivotal in our everyday decision making, such as punishment and reward. In the original paradigm used by Filimon and colleagues (2013), subjects responded without receiving any positive or negative feedback. On one hand, the punishment level for incorrect responses could have been parametrically manipulated across blocks of trials (as in Blank et al. 2013). On the other hand, a tiny modification in the paradigm (i.e., visual signal on the screen or auditory pleasant stimulus when the correct answer is given) can allow the research-
ers to gain insights from the influence of positive rewards on the decisional outcome. These results provide a mechanism of how prior expectations may affect perceptual decision making, namely by changing neural activity in, and sensory drive to, prefrontal areas.

Given the neural differences between young adults and elder people in decisional processing (Crone and Ridderinkhof 2011) and the relatively low age of the experimental subjects tested by Filimon and colleagues (2013) (24.9 yr, and a rather dispersed range of 20–32 yr), these results need to be replicated in an older, bigger, and more clustered representative population sample. It would also be productive to extend this study to adolescents, and thus to interpret motor plans and perceptual decision throughout their evolutive trajectories (Koolschijn et al. 2011).

Considering the social nature of decision making, the introduction of a trial-by-trial feedback to the experimental subjects could also be used to model real or fictitious social interactions by making the subject consider the presence of a potential competitor who plays the same paradigm, but with decisional outcomes that should be independent for every subject. This further modification coupled with the experimental timing used by Filimon et al. (2013) would also be useful to monitor the performance of the subjects, and it would result in an increase in response accuracy, mirroring an increase in their motivation aimed at making the right decision trial by trial, and intercepting the social side of decisional processes.

In real life, we are supposed to make decisions quickly, and, quite often, in a stressful social environment, different from the nonstressful experimental timing context used by Filimon et al. (2013). Therefore, to further complete this scenario, future research on decision making will also have to take advantage of the recent findings from the emerging research field of psychoneuroimmunology (see Eisenberger 2012). In this case, to further study the link between social relationships and physical health while performing decision-making tasks, the level of proinflammatory cytokines IL-6 and the soluble receptor for tumor necrosis factor-α (sTNFαR II) that are usually increased in competitive social interactions (Chiang et al. 2012) can be assessed. Finally, this level of analysis should be coupled with a more specific investigation of the oscillatory activity in the motor cortex at different frequency ranges during the decision-making process, to further exploit the dynamics of perceptual choice, and also those relating to expectation, a crucial component in our daily decisions (de Lange et al. 2013).

The accomplishment of a very detailed neurophysiological understanding of the decision-making process is possible only with a stimulating convergence of several levels of studies, with multiple experimental strategies linked to an interplay between studies on monkeys and on humans as well as a tight coupling of hypothesis-driven and bottom-up approaches. With the aim of depicting new theories of decision making, future research will not only have to record neurophysiological correlates of decision making and the interactions between cerebral areas, but also the modulations underpinning neural circuitry and oscillatory activity with magnetoencephalography and transcranial stimulation tools (i.e., TMS), putting hypotheses on functional brain architecture models, including the brain deep nuclei (Ding and Gold 2013), to the test.

In conclusion, real life decisions mix perceptual, social, and reward-based decision processes. Remarkable works such as this by Filimon and colleagues (2013), through carefully studying specific elements of the bigger picture, are incrementally extending the boundaries of our knowledge in this area. To properly interpret the complexity of this topic, we need to multiply the perspectives from which we can study decision making, before integrating all the newly acquired pieces of evidence into novel theories on this subject. Intriguing research avenues stand in front of us: it is time for neuroscientists to make challenging decisions on decision making.

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DISCLOSURES

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AUTHOR CONTRIBUTIONS

S.S. conception and design of research; S.S. analyzed data; S.S. interpreted results of experiments; S.S. prepared figures; S.S. drafted manuscript; S.S. edited and revised manuscript; S.S. approved final version of manuscript.

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