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Human posterior parietal cortex mediates hand-specific planning

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ABSTRACT

The processes underlying action planning are fundamental to adaptive behavior and can be influenced by recent motor experience. Here, we used a novel fMRI Repetition Suppression (RS) design to test the hypotheses that action planning unfolds more efficiently for successive actions made with the same hand. More efficient processing was predicted to correspond with both faster response times (RTs) to initiate actions and reduced fMRI activity levels — RS. Consistent with these predictions, we detected faster RTs for actions made with the same hand and accompanying fMRI-RS within bilateral posterior parietal cortex and right-lateralized parietal operculum. Within posterior parietal cortex, these RS effects were localized to intraparietal and superior parietal cortices. These same areas were more strongly activated for actions involving the contralateral hand. The findings provide compelling new evidence for the specification of action plans in hand-specific terms, and indicate that these processes are sensitive to recent motor history. Consistent with computational efficiency accounts of motor history effects, the findings are interpreted as evidence for comparatively more efficient processing underlying action planning when successive actions involve the same versus opposite hand.

Introduction

Human behavioral evidence suggests that the mechanisms underlying action planning are sensitive to recent movement history. For example, the ways that objects are grasped partly reflect recent grasp history (Cohen and Rosenbaum, 2004, 2011; Dixon et al., 2012; Kelso et al., 1994; Rosenbaum and Jorgensen, 1992; Schutz et al., 2011; Short and Cauraugh, 1997). Similar effects of recent motor history have been shown for the spatial paths of arm movements during successive reaching actions (Jax and Rosenbaum, 2007), the coordinated patterns of bimanual rhythmic finger movements (Kelso, 1981, as cited in Weiss and Wark, 2009), and the movement characteristics of paddle swings during table-tennis (Sorensen et al., 2001). According to some accounts, motor history effects reflect more efficient planning when recently executed motor programs are reused as opposed to newly specified (Rosenbaum et al., 2012). Here, we refer to this hypothesis as the planning efficiency account of recent motor history effects, and define better efficiency as faster planning associated with reduced neural processing costs when recently specified sensorimotor parameters can be reused.

We recently provided additional support for this account (Valyear and Frey, 2014). We showed that response times (RTs) to initiate successive actions are faster when the same versus alternate hand is used, even though those actions involved distinct grasps and object placement movements to distinct locations. These findings provide critical support for the planning efficiency account; in particular, since prior evidence reveals that actions are (at least partly) planned in advance of movement onsets (Klatzky et al., 1995; Pellegrino et al., 1989; Stelmach et al., 1994; Sternberg et al., 1978). In line with this framework, we interpreted our results as arising from repetition-related computational gains in the processes that underlie hand-specific planning.

Consistent with the hypothesis that repeated elements of successive actions are planned more efficiently, the above behavioral findings parallel newer evidence showing reduced fMRI signal levels for repeated hand actions within parietofrontal areas governing action planning. These effects, known as fMRI repetition suppression (fMRI-RS), have been shown for repeated grasping (Kroliczak et al., 2008; Monaco et al., 2011, 2014) and manual gestures (Chouinard and Goodale, 2009; Dinstein et al., 2007; Hamilton and Grafton, 2009). Critically, fMRI-RS has been linked to more efficient neuronal-level processing (Grill-Spector et al., 2006; James and Gauthier, 2006; Wiggs and Martin, 1998), and thus, these prior results are consistent with planning efficiency accounts of behavioral effects of recent motor experience.

Repetition-related decreases in the firing durations of neurons encoding action plans could explain both fMRI-RS and decreased response times to initiate actions. For example, if planning mechanisms operate in an activity-threshold-dependent manner (Cisek, 2007; Hanks et al., 2006), then changes in baseline activity levels according to recent motor history could account for faster planning and shorter durations of neural firing. Motor history can modulate baseline activity in neurons underlying the control of saccadic eye movements and these changes correlate with saccadic reaction times (Fecteau and Munoz, 2003).

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The purpose of the current study was to provide evidence for concurrent repetition-related decreases in response times to initiate actions and fMRI-RS within areas underlying action planning. Despite the relative prevalence of evidence for both behavioral motor history effects and fMRI-RS for repeated actions, to our knowledge, no study to date has demonstrated both effects concurrently.

Specifically, our primary aim was to provide a critical test of the planning efficiency account of our prior behavioral results showing RT differences according to recent hand-use history (Valyear and Frey, 2014). The efficiency hypothesis predicts that these RT effects will be accompanied by fMRI-RS within areas implicated in action planning.

The anatomical specificity of our predictions should be clear, and is worth emphasis. If faster RTs for repeated use of the same hand reflect more efficient planning, then fMRI-RS effects should be localized to those brain areas underlying action planning. Our task involves reaching, grasping, and object manipulation. As such, predicted areas correspond with those that have been implicated in reach, grasp, and manual object manipulation planning — bilateral posterior parietal and frontal premotor areas, including anterior/posterior intraparietal, superior/inferior parietal, and dorsal/ventral premotor cortices (Astafiev et al., 2003; Beurze et al., 2007, 2009; Gallivan et al., 2011; Jacobs et al., 2010; Marangon et al., 2011).

A second major aim of this study was to investigate the potential specificity of fMRI-RS for actions made with the same versus alternate limb, and in turn, the potential for *across-limb* RS effects. Prior research in this area has been limited to the study of repeated (versus non-repeated) elements of actions involving the same limb. To test for possible *limb-specific* RS effects, conditions involving successive actions with the same versus different limbs must be compared. This was a second new and important contribution of the current study.

Materials and methods

On each trial, participants performed pairs of successive actions – a prime and probe – involving unimanual object rotation movements with either hand (Fig. 1). Which hand was to be used and which direction objects were to be rotated depended on a set of arbitrary rules defined by the shape of objects. Four conditions were defined by the relationship between prime and probe events: either the same actions were repeated (Identical Repeat, IR), hand was repeated but grasp posture was changed (Hand Repeat, HR), grasp posture was repeated but hand was changed (Grasp Repeat, GR), or neither hand nor grasp posture were repeated (No Repeat, NR) (Fig. 1C).

Conditions involving repeated (IR and HR) versus non-repeated (GR and NR) hands were predicted to result in more efficient planning, as evidenced by: 1) faster response times (RTs) to initiate actions, and 2) fMRI-RS within parietofrontal brain areas known to underlie action planning.

In principle, more efficient neural processing may have also been detected for repeated grasps for successive actions involving alternate hands — i.e. for the GR condition. We addressed this possibility with the contrast: NR > GR. Such results would have provided evidence for effector-independent levels of grasp planning, shared across hands during successive actions.

Subjects

Twenty-one healthy individuals participated in the study. Data from one participant ware excluded due to non-compliance with the task (i.e. video data showed a high percentage of trials where bimanual actions were used to manipulate objects). The remaining twenty (6 female) participants were between 19 and 54 years of age (mean age = 28 ± 8.5 years). All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971), and provided informed consent in accordance with the local IRB and the Declaration of Helsinki. One participant had vision problems in one eye; estimated 10% vision available in the affected eye, due to a welding accident at the age of 18. He was 35 years of age at the time of testing. All other participants had normal or corrected-to-normal vision. None of the participants had any prior history of psychiatric illness, and all participants were naïve to the goals of the study. The experiment took approximately 3 h to complete (including pre-scan training), and participants received financial compensation for their participation.

Stimuli and presentation setup

Four novel objects were used, made up of simple 3D shapes – sphere, cube, triangle, and plus-sign – affixed to 6.5 (length) × 2.5 (width) × 1.7 (depth) cm handles (Figs. 1B/C). The use of the same handle dimensions for all objects ensured that differences in hand configurations used to manipulate objects were not related to differences in the physical properties of their handles. Duplicates of each object were included in the set so that even when identity was repeated within trials, the experimenter exchanged objects and the turntable was rotated.

Objects were presented using the platform and turntable apparatus shown in Fig. 1 (revised from Valyear et al., 2012). There were two sides of the apparatus that allow for independent presentation of prime and probe events. Each side comprised a workspace where objects were attached centrally and could be rotated clockwise or counterclockwise. The platform was specifically adjusted for each individual so that objects and the workspace could be comfortably viewed through mirrors, and so that objects could be manipulated with minimal movement of the arm. Specifically, the setup allowed participants to reorient objects without the need to move their upper arm or shoulder. Performing hand actions without shoulder movement effectively minimizes potential for movement-related artifacts (Culham, 2004). Response pads were fitted into plastic casings mounted to the apparatus, positioned to the left and right of the workspace. The distance from left/right response pads to objects was ~19 cm, on center. In the rest position, participants lightly pressed on the top surface of each response pad with their left/right hands (Fig. 1A). Button releases provided measures of response times to initiate movements, and were used to identify error trials where both hands were moved (see Videos).

Participants were instructed to fixate a small light source from a light-emitting diode (LED) transmitted via a single optical fiber attached to an adjustable plastic stalk positioned directly (~2 cm) above where objects were presented (Fig. 1A). For both prime and probe events, objects were made visible by brief (500 ms) illumination of a super-bright white LED transmitted via a bundle of five optical fibers attached to a second adjustable stalk. The experiment was otherwise carried out in complete darkness. An MRI-compatible infrared-sensitive camera (MRC Systems GmbH) was used to record participant's hand actions.

With the participant in position (with their head localized to the isocenter of the magnetic field), the apparatus remained outside the scanner bore. An experimenter stood next to the bore and manually replaced objects and rotated the turntable according to auditory cues conveyed through MRI-compatible headphones. The signal to replace prime objects and rotate the turntable occurred 2.5 s prior to the onset of prime events. Replacement of probe objects and rotation of the turntable for a second time then occurred during the 2.5 s delay period between prime and probe events. Although movements of masses within an MRI scanner's magnetic field can cause artifacts with echo-planar imaging (Barry et al., 2010), the experimenter's movements occurred outside (or nearly outside) the scanner's magnetic field and thus were not expected to result in any such artifacts. Also, experimenter movements were present for all trials; any potential artifacts would have affected all conditions similarly.

Procedure

Objects were presented with their handles oriented vertically, viewed by participants through the use of mirrors while they lay supine