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RESEARCH ARTICLE

Bias and sensitivity of proprioception of a passively felt hand path with and without a secondary task

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Abstract Previously, we observed changes in the scale, rotation, and location of drawn shapes when subjects simultaneously performed a secondary task, but not in the shape or proportion of the drawing. We suggested the secondary task impacted motor planning and execution or proprioception of the primary task. To isolate for proprioceptive effects, here we used the same secondary task during passive shape perception. A robotic manipulandum moved the subject's hand around the perimeter of a template shape and then a test shape differing in size, proportion, or location. Subjects also performed the same primary task while simultaneously performing a secondary task of reporting the orientation of right or left tilted arrows. We compared the performance between single and dual task, and different workspaces. In single-task conditions, subjects perceived scale, location, and proportion very close to the actual (all biases under 1 cm). A secondary task only increased the uncertainty range for judgment of scale, with no other effect. Subjects judged shapes in the centered workspace to be smaller and closer relative to the template compared with those in the peripheral workspace, although in that workspace, it was more difficult to discern changes in the proportion of the shape. The result for scale in the current passive paradigm is not different from our active study in which efference copy was available. This suggests that the scale parameters of the shape, whether actively or passively encountered, are disrupted by task interference at the level of proprioception or sensory integration rather than motor planning and execution.

Keywords Proprioception · Passive movement · Attention · Secondary task · Motor planning · Shapes · Internal representation

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Introduction

Executing and monitoring a purposeful action requires a continuously updated estimate of the body's position in space as well as sufficient central resources to effectively generate movement and evaluate task goals. Performance of these processes can suffer in instances where resources are allocated between two tasks. In a previous experiment where subjects drew quadrilaterals on a graphics tablet, we found that adding a secondary task did not affect the proportion (length-to-width ratio) and pattern of the shape, but did affect its scale. Location and orientation in external space were also affected with the additional task load (Martin and Henriques 2010). A question remained, however, whether the decrement to the location and orientation was due to overloaded proprioception or overloaded mechanisms for motor planning and execution. In comparison with voluntary movements, passive movements use no explicit motor plan or execution. In this study, we plan to investigate (1) how well people can use proprioception alone to discriminate differences between sequenced hand paths, and (2) whether sensitivity of the felt hand path is also impaired when accompanied by a secondary task.

Given that people show deficits in producing shapes, especially when faced with a secondary task, it is possible that in such a case, their ability to monitor and integrate proprioceptive information across time may be affected similarly or even to a greater extent. This may be partly because active movements involve not only this sensory feedback, but also efferent signals associated with generating the hand movement. Previous studies have demonstrated that hand or arm location judgments are performed more poorly when relying only on proprioception of the passively moved effector (Paillard and Brouchon 1968; Adamovich et al. 1998; Laufer et al. 2001). However, other research has shown that the addition of efferent signals associated with active displacement of the arm does not always lead to improved performance (Jones et al. 2010).

The effect of secondary attentional load on the perception of visual (Posner et al. 1980), auditory (Cherry 1953), and tactile (Soto-Faraco et al. 2004) information suggests that proprioception might be similarly affected. To date, no one has tested how proprioceptive acuity is impaired by a secondary task. For this preliminary study, we kept the shape very simple so we could be sure that subjects did not need to encode or memorize the shape and were able to concentrate on changes to its size, location, and proportion. Here, we first established baseline performance for sensing the path of a hand moved passively around the contour of a shape. Next, we investigated how adding a second task might influence the ability to perceive the contour. Since there is no outgoing motor plan for the passively moved limb, any decrement caused by the load of the secondary task would be attributable to the disruption of the ability to monitor the movement, whether through proprioception or through comparison with a mental representation of the desired shape. We tested these ideas by using a task in which subjects had to judge the difference between two passively presented contours both with and without a secondary task.

Methods

Subjects

A total of 22 healthy students aged 18–43 (mean age 22.7), 12 females, participated in all trials and conditions, 16 in exchange for university course credit and the remainder as volunteers from our laboratory. A subset of 10 subjects performed the arrow control task, aged 18–37 (mean age 24), 5 females. All subjects were pre-screened for self-reported right-handedness, freedom from neurological and/or motor dysfunction, and had normal or corrected-to-normal vision. The subjects gave informed consent, and the experiments were conducted in accordance with the ethics protocols set forth by the York Human Participants Review Subcommittee.

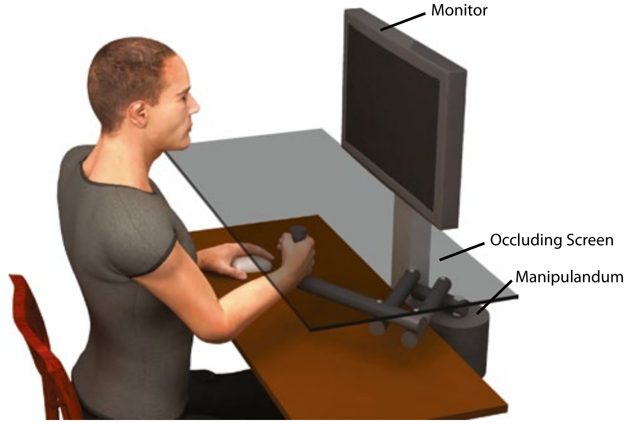

Fig. 1 Side view of the experimental setup. In the experiment, a drape occluded view of the arm and the occluding screen was opaque. (The drape is absent and occluding screen left transparent for illustration purposes). The manipulandum presented the shapes by passively moving the unseen hand, and in secondary task conditions, *arrows* were presented on the computer monitor

Apparatus

Figure 1 illustrates a side view of the experimental setup. For all conditions, subjects were seated in a dimmed room at a modified table equipped with a two-joint robotic manipulandum (Interactive Motion Technologies Inc., Cambridge, MA, USA). Height and distance from the table were adjustable by means of a locking chair, so the subject could comfortably reach all positions used by the manipulandum in this experiment. With the right hand, the subjects grasped the vertical handle of the manipulandum and were told to allow the robot to guide their hand around a shape. The manipulandum used a bell-shaped velocity profile to create each side of an 8 cm^2, positioned on or 8 cm to the right of the subject's body midline, ~30 cm in front of the subject's body at the midline. Throughout the experiment, a horizontal occluding platform blocked the view of the hands and a black cloth was draped from the subject's shoulder to the platform, hiding both arms. A computer mouse, affixed to the table, recorded subject responses during the dual-task conditions of this experiment. In single-task conditions, subjects placed the left hand on the left leg, below the mouse location. A computer monitor (model: Samsung 510 N, refresh rate: 72 Hz) was installed 17 cm above the table and centered on the subject's midline. All visual data for the secondary task conditions were presented on the monitor.

Procedure

For each trial in each condition, the robot presented two shapes consecutively and the subject was required to determine the difference between the first (template) and second (test) shapes. The trial sequence began with the subject

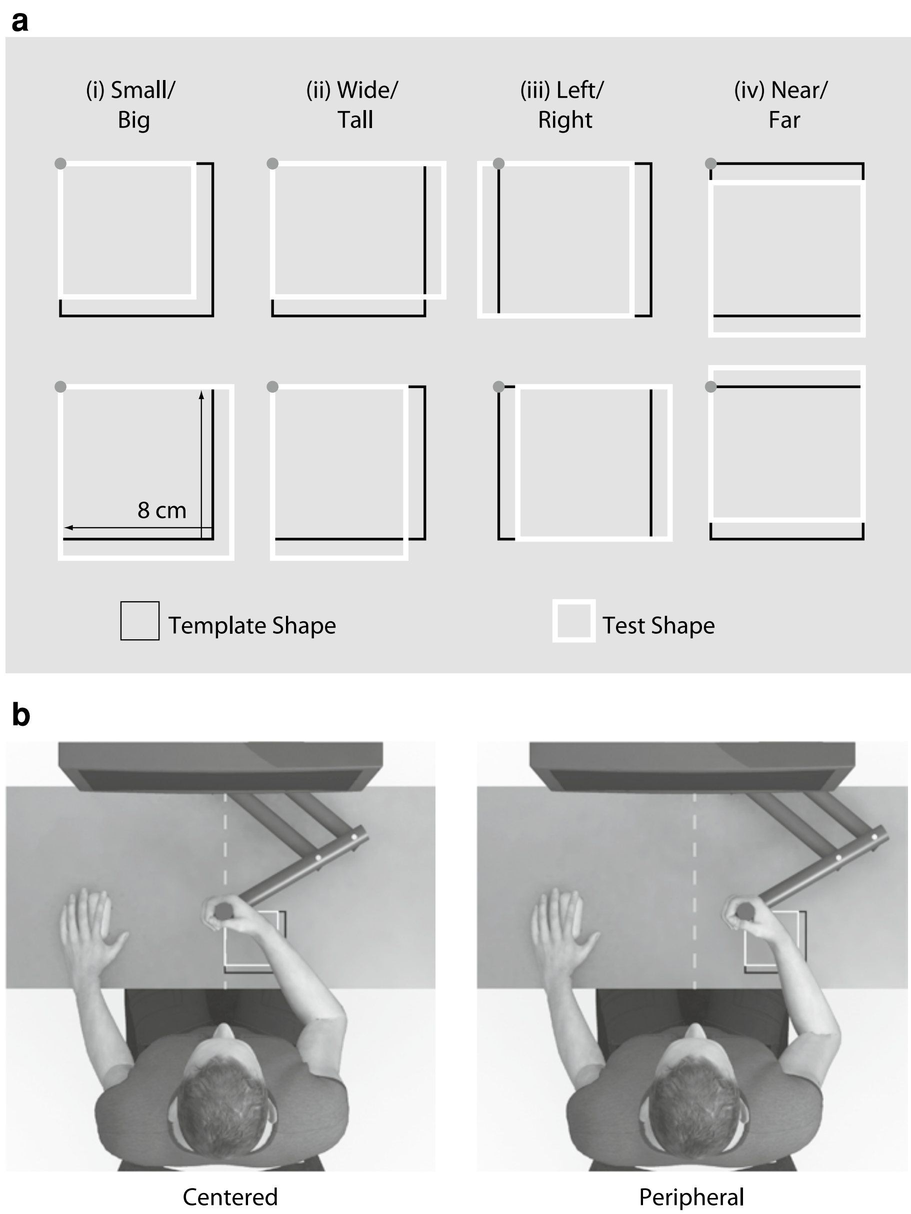

Fig. 2 Experimental conditions. **a** The *black wireframe* shows the 8-cm square template shape, and the *white wireframe* shows the manner in which the test shape was altered from the template for each condition, in this scale illustration, 1 cm different from the template. The *dot in the upper left hand corner* shows the start position for each trial. **b** Central *(left panel*) and peripheral (*right panel*) start position showing a trial from the small/big condition. *The dashed light gray line* shows the center of the workspace

seated in the chair and grasping the manipulandum. The robot moved the subject's hand to either the centered or right start location, and after a 0.5-s pause, it moved the subject's hand around the contours of an 8-cm template square in a clockwise direction, starting from the top-left corner of the shape so that each side took 1000 ms to complete. Following immediately after the presentation of the template shape, the robot presented the test shape, which differed from the template according to a specific parameter for each condition (described below). The robot paused and the computer generated two beeps, signalling the end of the movement. Then, using a two-alternative forced choice (2AFC), the subject verbally indicated the change they believed had occurred and the choice was recorded by an experimenter with a button press on a standard keyboard.

Conditions

In blocks, we separately tested four parameters of passive shape perception (depicted in Fig. 2a). All paths began and finished at the top-left corner of the shape. The small/big (Fig. 2ai) condition was tested for the perception of changes in scale, with the test shape having a bigger or smaller perimeter than the template shape. Larger shapes extended both further rightward and closer to the subject than the template shape, while smaller shapes were drawn within the boundary of the template shape, keeping its top and left edges. The wide/tall (Fig. 2aii) condition tested the perception of the proportion of the shape. A "wide" shape extended past the right edge of the template, with the near edge inside the boundary of the template, while for the "tall" shape, the right edge was inside the boundary of the template with the bottom edge below the template boundary. Left/right (Fig. 2aiii) tested the perception of translations in the centroid of the shape to left or right of the target with both side edges shifted leftward or rightward of the template. For example, in the case of a trial in the left-shifted test shape, the robot may have moved 7 cm across the top edge, drew the right edge 1 cm to the left of the template, made an 8-cm line across the bottom, and then drew the left edge to the top-left corner. The left edge was also 1 cm to the left of the template. Similarly, the near/far condition tested the perception of translations of the target closer to the subject relative to the target and further from the subject relative to the target. For near/far shapes (Fig. 2aiv), both the top and bottom edges of the shape were moved closer or further. The shapes were pseudorandomly presented either centered on the subject's midline, or at a peripheral location, translated 8 cm to the right (Fig. 2b).

In each block, we determined the point at which subjects were equally likely to judge the test shape as being smaller or bigger, wider or taller, further left or right, or nearer or farther relative to the target. We accomplished this by presenting two corresponding staircases for each member of the pairs, with each staircase being independently and randomly interleaved within the block, for a total of 80 trials. The initial test shape in each staircase was 4 cm (50 %) different from the template shape, and the initial step size was 1 cm. The size, location, or proportion of the test shape was adjusted over the block of trials in response to the subject's responses using an adaptive algorithm (Kesten 1958). If for example the subject was determining small/big difference, the test shape was adjusted until there was an equal probability that the subject would respond it was smaller or bigger than the template shape.

No-secondary task and secondary task conditions

Each parameter was tested by itself, as described above (the "no-secondary task" condition), or simultaneously with a mouse-clicking task in response to angle identification (the "secondary task" condition). In the secondary task condition, the robot guided the subject's hand around the template shape, and then, during the presentation of the test shape, arrows pointing to the left or right of vertical were randomly displayed on the video screen. Subjects responded to each arrow by clicking on the mouse buttons: left or right, respectively, to indicate the arrow was tilted to the left or right of vertical in a 2AFC. The amount of tilt varied from vertical by ±3°, ±5°, or ±10°. Arrows were continuously provided for the duration of the test shape presentation, with a random inter-stimulus interval between 500–1500 ms. If the subject did not respond to the arrow within 1500 ms (a miss), it disappeared and another appeared at the end of the inter-stimulus interval. The software recorded correct, incorrect, and missed responses, as well as the latency between the presentation of the arrow and the subject's response. As in the no-secondary task condition, at the end of the trial, the subject verbally reported in what way the test shape had changed from the template. In a separate arrow control condition, subjects performed the clicking in response to arrow angles task, without the passive shape perception task. In this condition, the subjects' right hands rested on their laps just below the workspace. The subjects performed 300 clicks in response to the arrow angle stimulus.

Data analysis

To determine whether the estimate of location or distortion at which the subjects were equally likely to report the test shape was left/right, near/far, small/big, or wide/tall relative to the target, we used a custom adaptive staircase algorithm which responded to user choices until the subject was equally likely to respond to either possible choice. The staircase for a typical subject in the small/big condition is shown in Fig. 3a. A logistic function was fit to the data for each judgment in each block, and from the logistic data, we calculated the point of subjective equality (PSE), the point at which the shape equally felt smaller or larger (black dashed line Fig. 3b), and the uncertainty range, or the difference between which subjects' response probability was 75 % to one side of the actual shape to 75 % to the other (gray dashed lines, Fig. 3b).

We compared the PSE and uncertainty results for each subject in each condition, using a two-way repeated measures ANOVA (RM ANOVA) with "no-secondary task" and "secondary task" conditions as one factor and the start location as the second. In no instance was there any interaction between the two factors, so we pooled the start location results to test our principal hypotheses regarding the addition of a secondary task. To determine whether the performance without secondary task was reliably different from the template, we also separately compared the PSE against zero for each condition (pooled for centered and peripheral conditions) in single sample, two-tailed t tests. We separately examined the performance of the clicking task, both as the only task and while performing each of the four primary passive shape judgment tasks. For each arrow angle (±3°, ±5°, ±10°), we pooled the data for left and right oriented arrows and calculated correct, incorrect, and missed responses as a percentage of all responses for each of the four secondary task conditions and the control arrow task. Each response type was analyzed in a separate 3 (angles, within group) × 5 (conditions, between group) RM ANOVA. The latency between the presentation of the arrow and the subjects' responses was examined in a 3 (angles, within group) × 5 (conditions, between group)

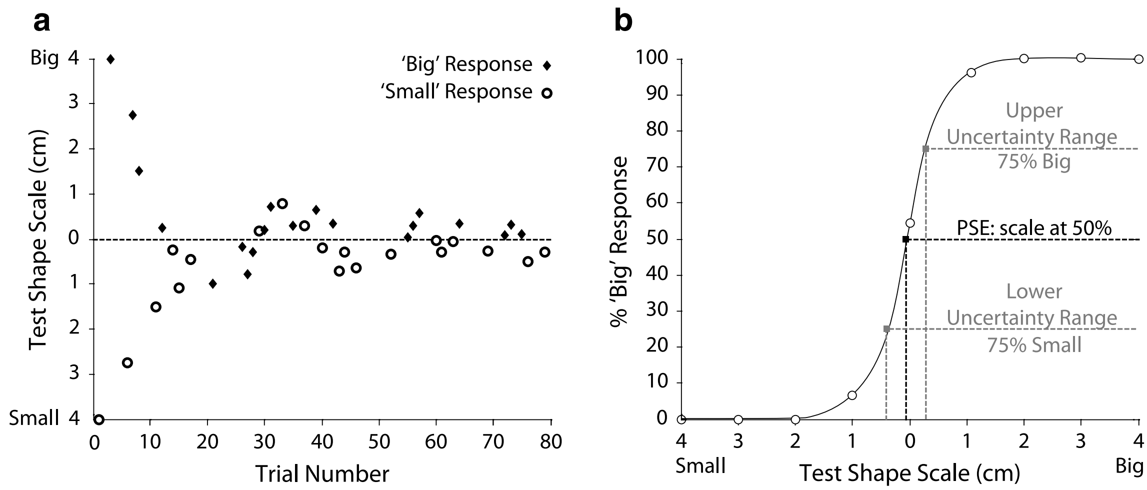

Fig. 3 Staircase of responses for a typical subject. **a** Using a custom, 2AFC adaptive staircase algorithm, we progressively changed the test shape relative to the 8-cm template square. *Markers below or above the line* indicate the test shape was actually smaller or larger than the test shape. **b** We fit a logistic function to the data for each subject to determine the bias, or point of subjective equality (PSE, *black square*) at which the subject was equally likely to answer that the test shape was smaller or larger than the template. The *dotted lines* indicate the points at which the subject was 75 % certain the test shape was either smaller or bigger than the template, with the area between showing the subject′s "uncertainty" range

× 3 (response types) RM ANOVA. We pooled the data for centered and peripheral workspaces in both of these analyses of the secondary task as these differences were not relevant to our hypotheses.

Results

We measured subjects' ability to detect changes in the scale, location, or proportion of a passively presented shape, both with and without an additional attentional load. Overall, subjects were very accurate when sensing changes between the template and test shapes, usually within a fairly small range of uncertainty. All means deviated from the template less than 1 cm for any measure, although only the wide/tall and near/far biases differed significantly from the template. Subjects were equally likely to judge the shape as wider or taller when it was actually 0.36 cm taller (7.64 cm wide × 8.36 cm high, $t_{21} = 2.12$, $p = 0.046$). In the near/far condition, subjects equally judged the shape as nearer or further when it was actually 0.79 cm nearer to them ($t_{21} = -4.05$, $p = 0.001$).

Effect of secondary task

When judging the relative scale of two passively presented shapes (small/big condition), subjects' uncertainty range nearly doubled when they simultaneously performed a secondary task ($F_{1,21} = 5.03$, $p = 0.036$), as depicted in Fig. 4. The black wireframe shows the mean size at which subjects were equally likely to judge the test shape as being either smaller or bigger than the template, and the gray area shows the range of uncertainty, that is, when subjects were less than 75 % certain that the shape was either smaller or bigger. For no other condition did the secondary task impact either the bias or the uncertainty range (Table 1, left column).

Effect of workspace

In each block, we pseudorandomly varied the start position to be either centered or translated 8 cm right. When

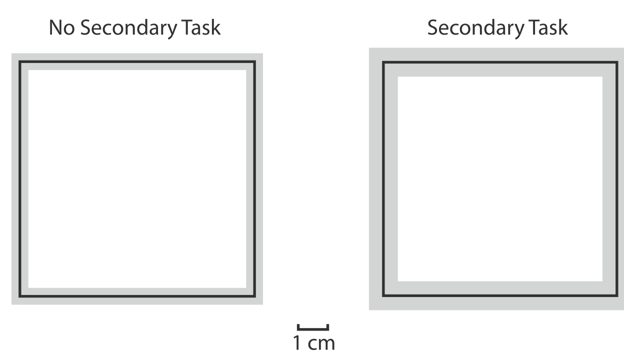

Fig. 4 Uncertainty range for test shape scale. Main effect of secondary task on the uncertainty range for detecting differences between scale of template and test shapes. Wireframes depict the point at which subjects equally judged the test shape to be bigger or smaller than the template, the PSE. The *wide gray line* shows the upper and lower bounds of the range of uncertainty, the area in which subjects were <75 % certain that the test shape was either larger or smaller than the test shape

Table 1 Comparison of task means by task load and workspace

Condition	Task bias		Sig.	Workspace bias		Sig.
	NST	ST		Cent.	Peri.	
Small/big	−0.05 (0.07)	−0.09 (0.01)	$p = .76$	*−0.17 (0.09)*	*0.03 (0.09)*	$p = .014$
Wide/tall	0.36 (0.17)	0.77 (0.16)	$p = .66$	0.61 (0.14)	0.52 (0.11)	$p = .43$
Left/right	−0.26 (0.24)	−0.07 (0.40)	$p = .11$	0.29 (0.38)	−0.61 (0.30)	$p = .07$
Near/far	−0.79 (0.19)	−0.79 (0.30)	$p = .99$	*−0.90 (0.20)*	*−0.67 (0.20)*	$p = .009$
Condition	**Task uncertainty**		**Sig.**	**Workspace uncertainty**		**Sig.**
	NST	ST		Cent.	Peri.	
Small/big	*±0.57 (0.11)*	*±0.98 (0.11)*	$p = .036$	±0.63 (0.11)	±0.65 (0.13)	$p = .66$
Wide/tall	±0.74 (0.17)	±0.88 (0.18)	$p = .23$	*±0.73 (0.14)*	*±0.85 (0.16)*	$p = .04$
Left/right	±1.55 (0.70)	±1.6 (0.46)	$p = .91$	±0.1.48 (0.38)	±1.65 (0.62)	$p = .56$
Near/far	±0.93 (0.17)	±0.1.04 (0.22)	$p = .41$	±0.99 (0.22)	±0.85 (0.14)	$p = .89$

Comparisons of mean difference from the template shape in centimeters followed by standard error of the mean (SEM) in brackets for the main effects of attentional load (no-secondary task (NST) or secondary task (ST)) in the left group of columns and workspace (centered or peripheral) in the right group. Significant differences for main effects of attentional load or workspace for a given condition are listed in italics. No condition was compared against any other

the workspace was centered, in the small/big condition, subjects were equally likely to judge the test shape as being bigger or smaller when it was actually 0.17 cm smaller, while in the peripheral space, the point of subjective equality was 0.03 cm bigger than the test shape (Fig. 5a, $F_{1,21} = 0.27$ $p = 0.014$). Likewise, for the near/far condition, shapes presented in the centered workspace were equally judged as nearer or farther than the test shape when they were 0.9 cm nearer, while the same judgment was made at 0.67 cm nearer than the test shape in the peripheral workspace (Fig. 5b, $F_{1,21} = 8.23$ $p = 0.009$).

When the proportion of the shape was altered (wide/tall condition), the overall PSE was reliably different from the template shape (Table 1). In this condition, subjects also had a greater range of uncertainty of whether the test shape was wider or taller when the shape was in the peripheral workspace ($F_{1,21} = 4.58$ $p = 0.04$). In the centered workspace, the PSE for the mean shape was 7.39 cm wide × 8.61 cm high (black wireframe, Fig. 6, left) and the uncertainty range was ±0.73 from that (dashed and dotted lines for lower and upper range, respectively). In the peripheral work space, the PSE for the mean shape was 7.48 cm wide × 8.52 cm high and the uncertainty range was ±0.85 cm (Fig. 6, right). All mean values of bias and uncertainty as determined by secondary task or workspace are summarized in Table 1.

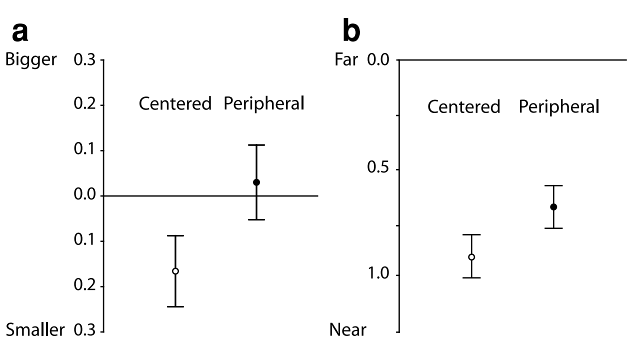

Fig. 5 Main effect of workspace on the bias of the small/big and near/far conditions. *White and black circles* show mean bias values for centered and peripheral workspaces, respectively; units in cm, *error bars* are SEMs. **a** The PSE for the scale of the test shape was smaller than the template shape in the centered workspace and larger in the peripheral. **b** The PSE for whether the shape had moved closer or further away was biased nearer the subject for both workspaces, but more so in the central workspace

Secondary task

For the secondary task, subjects viewed arrows presented at random intervals and spatial locations on the video screen, oriented at ±3°, ±5°, or ±10° to from vertical, and judged whether the arrows were pointing to the left or right. We compared their performance between the control task (performed without shape judgment) and the blocks of dual-task performance for three types of response: correct, incorrect, and missed responses. There was no main effect of condition for the number of correct, incorrect, or missed responses to the arrows: in other words, subjects were equally good at identifying the arrow orientations regardless of whether they were performing this task alone or concurrently with the shape perception task. However, subjects were not able to score perfectly on the task, demonstrating that it did provide a challenge. We pooled values across all angles. Subjects responded correctly 75.8 %

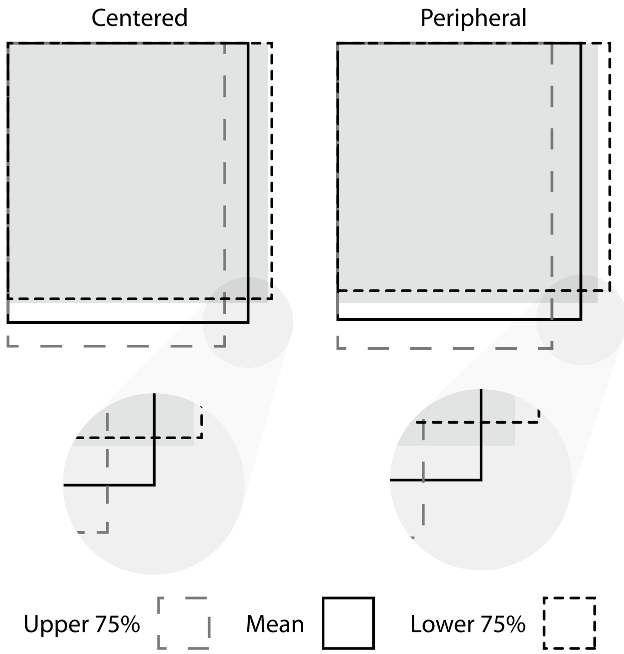

Fig. 6 Main effect of workspace on uncertainty of wide/tall condition. The *gray solid box* shows the proportion of the template shape, and the wireframe shows the proportion at which the subjects were equally likely to judge the shape as wider or taller. The *shorter dashed lines* show the point at which subjects were 75 % certain the shape was *wider* and the *longer dashed lines* when they were 75 % certain the shape was taller. The difference between the *dotted* and *dashed* shapes was greater in the peripheral workspace and was not changed by the addition of a secondary task. The inset shows the corner of each shape at ×2 magnification to better illustrate the differences

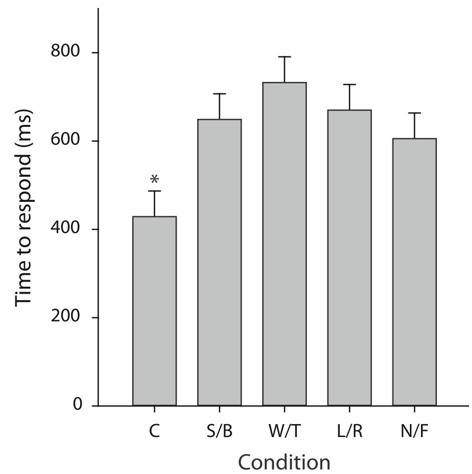

Fig. 7 *Arrow* response latencies. Comparison of response latencies by condition, from the time the *arrow* was presented until the response. The mean control condition response latency (*asterisk*) was faster than the mean of any dual-task conditions

of the time, incorrect 14.6 % of the time, and missed responses 9.6 % of the time.

Subjects were quicker at responding to arrows when they were not simultaneously judging changes to the shape. The latency from the presentation of the arrow until the response was the least for the control condition (429 ms) and greater for all dual-task conditions (Fig. 7: small/big, 648 ms; wide/tall, 733 ms; left/right, 670 ms; near/far, 605 ms; $F_{4,135} = 4.935$, $p = 0.001$, all comparison with a modified Bonferroni correction, $p < 0.017$). Across all conditions, subjects took longer to respond to the 3° arrow than either 5° or 10° (not shown, $F_{2,8} = 15.15$, $p < 0.001$ all comparisons $p < 0.001$). There were no interactions between arrow angle or response type with the condition factor.

Comparison with our previous active-drawing data

To understand the sensitivity of shape perception based on passive motion of the hand, we compared the no-secondary task condition of this experiment with the no-secondary task condition of our previous active shape-drawing paradigm. In that experiment, subjects made diamonds and squares shapes, both 4 and 8 cm in size, and also made more than one repetition of the shape. Fifteen healthy right-handed subjects (10 males, ages 17–40 years, mean age 23.3) with normal or corrected-to-normal vision participated as volunteers in that experiment (Martin and Henriques 2010). We selected all 8-cm test squares after only one repetition (no template squares) so that we could more directly compare the two experiments, shown in the table below (Table 2, previously unpublished data). We expressed all values for all measures as an absolute difference from the template shape (as a ratio for the scale and proportion measures, and in cm for the drift measures), so we could answer the question: Did one condition result in a greater difference between the template and test shapes? If the absolute mean for a given measure is greater, then that condition likely caused more interference. We used independent samples *t* tests to compare the active and passive paradigms and found changes in scale were sensed more poorly in the active condition for both centered and peripheral start locations (centered: 0.29 for active vs. 0.04 for passive, $t = -4.11$, $p = 0.001$, peripheral: 0.26 for active vs. 0.05 for passive, $t = 4.38$, $p = 0.001$). By contrast, left/right drift was performed more poorly in the passive paradigm only in the centered start location (0.59 active vs. 1.46 passive, $t = †-3.0$, $p = 0.006$; Table 2). Performance was not different for any other measures for either active or passive conditions in either workspace.

Table 2 Comparison of no-secondary task conditions between previous and current experiment

	Active	Passive	Unpaired *t* test results				
	Mean (SD)	Mean (SD)	*F*	Levene's	*t*	*df*	Sig.
Centered							
Small/big	*0.29 (0.24)*	*0.04 (0.04)*	*17.26*	*0.00*	*4.11*†	*14.45*	*p* = .001
Wide/tall	*0.59 (0.45)*	*1.46 (1.25)*	*5.09*	*0.03*	*−3.00*†	*28.22*	*p* = .006
Left/right	1.11 (0.61)	1.16 (0.76)	0.80	0.38	−0.20	35.00	*p* = .844
Near/far	0.09 (0.08)	0.08 (0.09)	0.07	0.80	−0.40	35.00	*p* = .694
Peripheral							
Small/big	*0.26 (0.18)*	*0.05 (0.04)*	*31.87*	*0.00*	*4.38*†	*14.70*	*p* = .001
Wide/tall	0.57 (0.40)	0.93 (0.74)	6.15	0.02	−1.87†	33.62	*p* = .070
Left/right	1.21 (0.47)	0.83 (0.68)	2.29	0.14	1.86	35.00	*p* = .071
Near/far	0.10 (0.05)	0.08 (0.07)	0.80	0.38	0.52	35.00	*p* = .605

Comparisons between our previous active-drawing experiment and our present passive-sensing experiment of the absolute mean difference from the template shape followed by standard deviation (SD) in brackets for each measure when there was no secondary task. These calculations are separated by centered and peripheral workspace. Area and proportion values are absolute mean differences from the ratio of performance relative to the ideal shape, and left/right near/far values are absolute differences from an ideally positioned shape, in cm. The left value column shows mean and standard deviation data from our previous active-drawing experiment (previously unpublished data) followed by transformed data from the present, passive-sensing experiment. Significant differences for main effects of attentional load or workspace for a given condition are listed in italics

† Where Levene's test for homogeneity of variances was significant, adjusted *t* and *p* values are provided in the table above

Discussion

We explored how bias or sensitivity to changes in a passively felt shape would be impacted by the addition of a secondary task. Since there is no outgoing motor plan, any decrement caused by the additional task load would be attributable to the disruption of the ability to monitor the movement, whether through proprioception or comparison with a mental representation of the desired shape. We tested these ideas by using a task where subjects had to judge the difference between two passively presented shapes both with and without a secondary task.

When judging a passively guided hand path for the changes to the scale or proportion of the test shape, or whether the test shape had moved to the left or right, the bias was so small that it was not reliably different from the template. In the near/far condition, where judgment of the test shape's location was reliably different from the template, the difference was just over half a centimeter. Subjects were also quite resistant to perturbation by a secondary task: in that case, subjects were less certain whether the test shape was smaller or larger than the template. The mean value or bias for each condition represents the point at which subjects were equally likely to judge differences in the test shape as biased toward either choice (smaller/bigger, wider/taller, left/right, near/far), termed the point of subjective equality (PSE). With or without a secondary task, in the centered workspace, the PSE for the small/big condition was smaller than the template and the PSE for the near/far condition was nearer than the template relative to their judgment in the peripheral workspace. In the peripheral workspace, subjects were also less certain of whether the test shape was wider or taller than the template.

Bias and sensitivity of the passively moved arm

We passively guided subjects' hands around the perimeter of two serially presented shapes. When there was no secondary task, subjects were very sensitive to changes in the proportion and location of two serially presented quadrilaterals, with the bias in all cases being less than 0.75 cm. The single-task measures in the passive experiment were performed with the same accuracy as in our previous active experiment. In the active experiment (Martin and Henriques 2010), simultaneously monitoring all of the shape and location parameters while drawing the quadrilaterals may itself have imposed additional load on processing or movement. In a previous experiment from a different group, subjects who were instructed to observe differences in a visual match-to-sample task were better able to identify shape changes when they only attended one parameter as opposed to many attributes (Corbetta et al. 1991), although it is unclear whether the same mechanisms used in a visual search task would be used in our motor task. Overall, however, writing behavior is fluid and adaptable with largely invariant shape components and variable spatial components (Bullock 2004), and preserves shape parameters even in the total absence of proprioceptive or visual feedback (Farrer et al. 2003). Moreover, we used a very familiar shape that from age four onward can be reliably reproduced (Otte and van Mier 2006).

Passive haptic shape recognition may have advantages not present in passive recognition of shapes by vision. An experiment by Craddock and others compared active and passive aperture viewing during an object recognition task. The visual image of the different shapes was revealed through a small window over time rather than instantly as when one normally sees an entire object. This is similar to the haptic shape exploration over time in our experiment. In their first condition, the subject actively controlled the movement of the window, while in later conditions, they viewed either the replay of their own movements over the shape, or the replay of another subject's movements. Active control of the aperture resulted in the fastest recognition times possibly, the authors speculate, because subjects were able to move the window over parts of the image providing the most useful information (Craddock et al. 2011). This might suggest that the hand movements in their active condition were most responsive to visual rather than proprioceptive feedback.

Despite these factors, the presence of an outgoing motor command does not appear to have given a specific advantage to performance in the previous active task. This corroborates other work from our laboratory, where subjects judged the end location of the hand after actively moving it along a 10 cm constrained channel, or after it was moved passively by a robot. In the active condition, the bias was 0.92 ± 1.74 cm, which was not significantly different from the passive condition (Jones et al. 2010). In the current experiment, however, the task was not a point and reach type movement, but a multi-segment movement pattern, which is more than just an aggregate of many reaches. The central representation of a shape in an active haptic exploration task is thought to be synthesized over time by reference to the previous element in the shape sequence (Henriques et al. 2004). This is in keeping with Lashley's theoretical construct of parallel preparation of serial acts, in which the entire sequence is prepared in advance (Lashley 1951) and has been observed in area 42 of the prefrontal cortex (PFC) in non-human primates (Averbeck et al. 2002, 2003).

Research has also identified activity in the lateral occipital complex (LOC) for the cortical representation of a shape, whether by vision or through haptic exploration (Peltier et al. 2007). This representation appears to be a higher level construction of the shape, rather than just a composite representation of its individual components (Kourtzi and Kanwisher 2001). Additionally, visual and haptic exploration of shapes activates similar networks including the primary somatosensory area (S1), the anterior supramarginal gyrus, and the intraparietal sulcus (IPS). These same areas are active whether the shape is actively or passively explored (Bodegard et al. 2003), and both in the act of encoding the movement or matching to a previous sample (Miquée et al. 2008). The anterior IPS and adjacent areas of the superior parietal lobule are also active while shapes are being held in short-term memory (Fiehler et al. 2008).

Importantly, simply thinking of shape characteristics related to presented words activates the inferior parietal lobule and the primary somatosensory area, presumably as parts of a distributed network that encodes shape representations based on both visual and somatosensory information (Oliver et al. 2009). Another study of the cortical representation of shape implicates the post-central sulcus (PCS), the intraparietal sulcus (IPA), and the posterior occipital complex (POC). Analysis of time course-dependent activity in these areas yields two equal models of their interrelated function: a top–down model which reveals a path from POC and parts of the IPS to the PCS, while the bottom–up model reveals a flow from PCS to IPS (Peltier et al. 2007). It is possible that the top–down model provides online correction for shape production, and that the bottom–up model compares incoming sensory information against a central representation. We propose that this flexible central representation may be used to provide the basis for comparison in both our passive and active experimental conditions. Such a representation would be available whether the task is to actively produce or to passively perceive the shape.

Interestingly, shape-related activity in the LOC, and its macaque analog, the inferior temporal cortex (IT), is invariant to changes in size. Single neurons in the macaque IT are responsive to the shapes of different complex visual stimuli, largely independent of the size or position of the shape (Schwartz et al. 1983). Populations of neurons in IT are also responsive to different rotated views of the same shape and for the most part invariant to location and size (Logothetis et al. 1995). An fMRI experiment with data from both human LOC and monkey IT shows considerable size invariance in each species, even when those brain areas adapted to the continuous presentation of the stimuli (Sawamura et al. 2005). In this way, both visual perception of shape and motor production demonstrate a similar distinction between the shape and size parameters of the perceived or drawn object.

Effect of secondary task

Adding a secondary task to the shape judgment task increased subjects' uncertainty about whether the test shape was smaller or bigger than the template shape. We observed no other effect on passive shape perception when simultaneously responding to the randomly presented arrows. In our previous, active experiment, the same additional task load caused decrements in scale and location of the test shape. Specifically, in that study, the addition of the arrow task increased the size of the drawn shape by up to 26 % of the template shape's size. Similarly, shapes in some of the dual-task conditions tended to be drawn ~0.5 cm more to the right ($p < .07$).

The effect of a cognitive load on proprioception has been previously reported, although it is not clear that the effect in that instance was due only to load on proprioception. Subjects performed a single-joint adaptation task alone or simultaneously with backward counting and were shown only the terminal position of the cursor relative to the target. Controls showed small (~0.5°) increases in errors when the counting task was added, in comparison with a deafferented patient who displayed much larger increases (>1.5°). The patient displayed different force and velocity profiles than controls during placement of the arm, suggesting a strategy not dependent on sensory feedback, but rather on the prediction of the arm's likely behavior (Ingram et al. 2000). However, in the case of the deafferented patient, additional load cannot possibly impact proprioception. The additional impairment with the cognitive task in that instance is more likely due to load on planning and execution mechanisms, which may also explain some of the deficit for the controls, rather than just proprioception, as claimed by the authors. Similarly, research with a different deafferented patient in a writing task demonstrated decrements to spatial components, but not the shape components of the writing when there was no vision of the hand (Farrer et al. 2003). The location parameters of the task appear to be dependent on feedback mechanisms, while the shape parameters appear to be dependent on an internal representation that is fed forward, largely independent of feedback. Such use of parameter-specific mechanisms may reflect a model that flexibly takes the best information to achieve task goals, whether the information is provided in a closed-loop manner through proprioceptive feedback or in an open-loop manner through use of a mental template (Scott 2004; Todorov 2004).

In our previous, active experiment, with an additional task load subjects drew the square smaller than the template shape, and in this experiment with an additional task load, they perceived a smaller test square as being equal in size to the template. This suggests that the subjects felt their hand paths to be larger than veridical when both passively judging and actively drawing these shapes. We previously hypothesized that some of the performance decrement in the active condition may have been caused by the secondary task's interference with motor planning and execution (Martin and Henriques 2010) and used the present passive paradigm to test whether planning and execution, proprioception or both may be responsible for the decrements. The secondary task was identical in both experiments; however, in the passive experiment, subjects made no motor plan for the primary task, yet still showed a decrement in performance for the scale of the shape. We propose that in the case of scale, the secondary task caused resource competition in processes other than motor planning and execution, most likely proprioception. Nevertheless, evidence from both experiments as well as others suggests that secondary task interference to motor planning and execution is also a contributing factor for some parameters, especially in our first experiment where more parameters were affected, and subjects also controlled more parameters. Further research will be necessary to disambiguate the interplay of these two features.

Effect of workspace

In the present experiment, subjects sensed shapes in either a workspace centered on the body midline, or translated 8 cm to the right. When comparing performance in the centered and peripheral workspaces, the point of subjective equality (PSE) for scale was smaller and for location was closer in the centered workspace. When a secondary task was added, no additional performance deficit was seen in either workspace. Surprisingly, however, in the peripheral workspace, shapes perceived as equal were closer to veridical than in the centered space. Studies examining reaches in contralateral and ipsilateral workspaces have found ipsilateral advantages for speed and timing, and precision (Carson et al. 1992), hypothesized in these studies to reflect an advantage based on the side of stimulus presentation. However, at least one study has demonstrated the ipsilateral advantages to be biomechanical rather than central (Carey et al. 1996). Our study only approached the midline, but did not cross into contralateral space, and furthermore, the movements were passive. Moreover, the scale of the shape was judged as smaller in the central workspace than in the peripheral one. Additionally, in the peripheral workspace, subjects were more uncertain whether the test shape was wider or taller than the template, although this measure did not differ in bias for the two workspaces.

Effect of the secondary task on the primary task

As in our previous, active paradigm, our secondary task was mouse clicking in response to arrows presented visually on a computer screen. Correct and incorrect responses regarding arrow orientation were no different when the clicking task was performed alone as a control or when it was performed as an adjunct to the primary shape change detection task; however, the task was sufficiently difficult that ~10% of the arrows were missed and ~15% were answered incorrectly. Moreover, in comparison with when subjects responded to the arrow task alone, subjects took longer to respond to the arrows in all dual-task conditions, demonstrating that there were behavioral effects for the secondary task as well. Equally, this secondary task previously caused reliable performance decrements in the active shape-drawing task. The task required subjects to use the left hand; however, they were instructed to rest the forearm or wrist on the work surface to provide optimal stability. It is unlikely that the relatively small movements of the index and middle fingers caused biomechanical effects resulting in impairment in scale judgment, and furthermore, the effect was also evident for a verbal responding condition in the previous experiment (Martin and Henriques 2010). Still, these tiny, simple mouse-clicking movements were able to cause a small but significant decrement in shape proprioception in the present experiment and it is possible that more complex movements would have similar or more dramatic effects.

Conclusion

We interact with objects everyday: in some cases, movement past or across the object will cause our hand, arm, or other body part to be in continuous passive contact with the object. Important spatial and environmental information can be derived from these encounters. Our proprioceptive systems are able to assess changes in these contours with considerable sensitivity even when we are not actively exploring the shape or producing a shape based on memory or a central representation of the shape. When even a very simple secondary task is introduced, passive sensitivity is affected for the scale parameter of the shape: attention to another task mildly impairs proprioception. The ability to sense or prevent changes to the shape, depending on whether the arm is passively or actively moved, suggests that high level representations of the shape may be available both for perception and action.

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