Neural Correlates of Individual Differences in Spatial Learning Strategies

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Behavioral studies have shown that spatial skills, such as mental rotation, are correlated with preferences for certain types of spatial information. To be more specific, better mental rotation is associated with a preference for survey (maplike) spatial information relative to route (landmark or wayfinding) information. Functional MRI was used to investigate how individual differences in spatial skills (mental rotation) interact with encoding information from these two spatial perspectives. Despite similarities in performance across individuals for route and survey learning, differences between route and survey encoding activation increased with increased mental rotation ability in anterior cingulate, middle frontal gyrus, and postcentral gyrus. This correlation appeared to be due to decreasing activation during survey encoding and not activation changes during route learning. The results suggest that mental rotation skill contributes to survey or map learning but that alternative strategies can be used under the circumstances of this study to achieve equal performance.

Survival is dependent on the ability to find one’s way in the environment, and different species have evolved different mechanisms for this purpose (e.g., sight, smell, and sonar). Humans learn the spatial layout of large-scale environments through many different methods, but two of the most common are maps and wayfinding (exploratory navigation). Behaviorally, these two types of spatial learning appear to lead to different ways of representing spatial knowledge that, in turn, result in different patterns of memory performance. For example, when people learn from maps, they are better able to make straight-line distance or direction judgments, whereas when people learn from wayfinding, they are better at estimating time on route (Moeser, 1988; Streeter, Vitello, & Wonsiewicz, 1985; Thordnyke & Hayes-Roth, 1982).

Neurologically, different brain regions may be responsible for different types of spatial processing. For example, the hippocampal region and parietal cortex have been implicated in processing allocentric and egocentric spatial information, respectively. Single-unit recordings in the hippocampus have suggested that neurons in this region are sensitive to location with respect to the larger environment in rats (e.g., O’Keefe & Nadel, 1978) and primates (e.g., Rolls, 1999). In humans, damage to the hippocampus produces global deficits in memory but has also been linked to specific problems in using allocentric information about space (for review, see Burgess, Jeffery, & O’Keefe, 1999). In contrast, neurons in the primate parietal cortex respond selectively to locations in various egocentric reference frames (e.g., Andersen, Snyder, Bradley, & Xing, 1997; Colby & Goldberg, 1999). Damage to this region in humans produces similar deficits in egocentric space in the form of hemispatial neglect (e.g., Burgess et al., 1999; Robertson & Marshall, 1993).

With regard to large-scale spatial learning, both allocentric and egocentric spatial information may be contributing to spatial learning. Deficits in large-scale spatial learning have been summarily labeled topographical disorientation, but damage to different areas of the brain can produce specific deficits that appear to reflect the use of different types of spatial information (Aguirre & D’Esposito, 1999). For example, patients with damage to the parietal cortex have difficulty representing the spatial locations of objects with respect to their egocentric position, whereas patients with posterior cingulate damage have difficulty representing locations in the external environment. Although both deficits can produce problems with navigation, they reflect injuries to different aspects of spatial learning.

In addition, functional imaging studies have used virtual reality to compare approximations of wayfinding (also called route learning) and maps (also called survey learning). Route learning involves encoding an environment from the perspective of a ground-level observer following a path through space, incorporating information over successive views and changes in orientation. In contrast, survey learning involves encoding an environment from an aerial perspective external to the space, panning over the environment from a fixed orientation. In the brain, the comparison of route and survey learning has revealed regions preferentially activated for the different types of encoding (Shelton & Gabrieli, 2002; see Figure 1). Stronger activation for route encoding was observed in bilateral medial temporal lobes (MTLs), bilateral postcentral gyrus (Brodmann Areas [BA] 5 and 7), right superior parietal cortex (BA 7), bilateral posterior cingulate (BA 31), right inferior parietal cortex (BA 40), left cuneus and middle occipital gyrus (BA 18), right superior temporal/insular cortex (BA 22 and 13), and left medial frontal gyrus (BA 6). Stronger activation for survey encoding was observed in bilateral fusiform and inferior temporal gyri (BA 37, 19), bilateral superior parietal cortex (posterior BA 7), left insula/claustrum (BA 13), and left superior...
frontal gyrus (BA 8). Differences in activation patterns have also been observed during retrieval following route and survey learning (Mellet et al., 2000).

Although these general differences in behavioral performance and neural correlates of maps and wayfinding suggest that humans process these two types of spatial information in distinct ways, research has demonstrated that different individuals tend to prefer different types of spatial information (e.g., Pazzaglia & De Beni, 2001). For example, some individuals prefer dealing with spatial information in terms of the landmarks along the route to be followed (specifying when and where to turn), whereas other individuals prefer to deal with space in terms of global reference points, such as cardinal directions (Lawton, 1996). Although both strategies tend to be efficient for successful wayfinding (Denis, Pazzaglia, Cornoldi, & Bertolo, 1999; Passini, 1984), the former reflects a preference for landmark and/or route information, and the latter reflects a preference for survey information. Moreover, the strategy preference has been closely linked to other spatial skill differences. In particular, participants who showed a strong preference for a survey strategy were significantly better on mental rotation of three-dimensional objects compared with participants who preferred more landmark-based strategies, suggesting that mental rotation ability predicts proficiency with survey information (Pazzaglia & De Beni, 2001).

The source of these individual differences and their impact on spatial learning have long been of interest to cognitive psychologists (e.g., Allen, Kirasic, Dobson, Long, & Beck, 1996; Brown, 1932; Hirstle & Hudson, 1991; Kozlowski & Bryant, 1977), but little is known about how these differences might be reflected in the underlying neural systems. On the basis of the strong relationship between mental rotation and strategy preference, one can hypothesize that individuals of varying mental rotation ability might process route and survey information differently.

In Shelton and Gabrieli (2002), fMRI revealed clear differences in brain activation between route and survey encoding. We designed the present study to investigate the degree to which those observed differences, as well as differences in other brain areas, were mediated by individual differences in three tests of spatial abilities. Participants were scanned while learning two different virtual environments, one as a route-based movie and one as a survey-based movie. Following encoding, participants were tested on their memory for the learned environments.

**Method**

**Participants**

Twelve healthy, right-handed volunteers (6 women, 6 men; M age = 23.1 years) participated in return for monetary compensation. All participants gave informed written consent.

The use of equal numbers of men and women allowed us to examine possible gender differences (e.g., Cutmore, Hine, Maberly, Langford, & Hawgood, 2000; Eals & Silverman, 1994). However, no significant effects or nonsignificant trends were observed on any of the behavioral or neuroimaging analyses. The lack of a gender difference may be due to the small sample size.
Materials and Procedure

Details of the experimental task are described elsewhere (Shelton & Gabrieli, 2002). In brief, three novel environments were constructed in desktop virtual reality using Virtus WalkThrough Pro (Virtus Corporation, Cary, NC). Two navigation movies were recorded for each environment, one from the ground-level perspective (route movie) and one from an aerial perspective (survey movie). One complete run of each movie lasted 46 s, and the same movie was used for a given environment throughout the encoding. Each participant was assigned to learn two different environments, one as a route movie and one as a survey movie. Prior to scanning, participants viewed the route and survey movies that would be used during the scan one time each. This initial presentation was used to familiarize them with the virtual reality presentation, during which time the landmarks were identified by the experimenter in the order they were encountered. During the scan, each of the two movies served as a 46-s block and was repeated six times. Route and survey movies were alternated in a pseudorandom order along with six 24-s blocks of fixation. During fixation blocks participants were instructed to fixate on a white cross in the middle of the black screen. Block order was determined by using all possible orders of conditions (route, survey, and black screen). Block order was determined by using all possible orders of conditions (route, survey, and black screen). Two different orders were used to counterbalance which environment was seen first (route or survey). Participants were asked to learn each environment as well as possible for a later memory test. They were also instructed to use the fixation periods to rest.

To assess whether environments were learned, we gave participants recognition memory tests for images of each environment. Participants saw still images of each environment from the route and survey perspectives and had to indicate whether the image was from the correct environment or from a distractor environment. Distractors were created by randomly rearranging the same landmarks within the environment. Participants judged a total of 64 correct images and 64 distractors for each environment.

Following the scan session, participants were asked to draw maps of the learned environments and given a brief postexperiment interview. Questions assessed which environment participants found most difficult, self-reported spatial ability, and self-reported facility with maps. Finally, participants completed three different pencil-and-paper tests, aimed at distinguishing different aspects of spatial skill. The Mental Rotation Test (MRT; Vandenberg & Kuse, 1978) assessed participants’ ability to mentally manipulate three-dimensional objects. The Road-Map Test (RMT; Money & Alexander, 1966) required participants to follow an imaginary route on a map, making left–right discriminations following mental translation and rotation of perspective. The Perspective-Taking Task (PT; Kozhevnikov & Hegarty, 2001) required participants to make judgments about relative locations of objects from imagined perspectives.

fMRI Data Acquisition and Analysis

Whole-brain imaging data were acquired on a 3 Tesla MRI Signa LX Horizon Echospeed (8.2 S system revisions; General Electric Medical Systems, Milwaukee, WI). Three-dimensional, high-resolution, T1-weighted SPGR anatomical images were acquired in 124 contiguous 1.5-mm slides (Min Full echo time [TE]; 30° flip angle; 24-cm field of view). T2-weighted spin-echo anatomical images were acquired in 29 contiguous 6-mm coronal slices (30-ms TE; 4,000-ms repetition time [TR]). Functional images were acquired in the same slices using T2*-sensitive gradient echo spiral pulse sequence (Glover & Lai, 1998; 30-ms TE; 2,000-ms TR; 76° flip angle; 20-cm field of view; 64 × 64 acquisition matrix). The functional scan lasted 12 min, during which time participants viewed the movies. Head motion was minimized with a bite bar using the participant’s dental impression.

Using SPM99 (Wellcome Department of Cognitive Neurology, London, United Kingdom), the data for each participant were corrected for motion, normalized to a T2-weighted template image, and smoothed with a smoothing kernel of 8 mm. Individual models were calculated for each participant using a general linear model (Friston et al., 1995). Contrast images for the difference between route and survey encoding from each participant’s model were subjected to random effects analyses (Holmes & Friston, 1998).

Two kinds of analyses were undertaken, a regions of interest (ROIs) analysis and a whole-brain correlation analysis. The ROIs were those that showed reliable differences between route and survey encoding (route > survey or survey > route); these regions were of a priori interest given the hypothesis that mental rotation skill would influence activation in neural systems engaged preferentially in survey spatial processing. The contrast between route and survey conditions had the limitation, however, that they were defined by differences that were consistent across all participants. Given the present focus on individual differences in spatial abilities, it was possible that activations in some areas would be highly variable (although systematically related to spatial abilities) and therefore not detected by group contrasts between conditions. Therefore, whole-brain correlation analyses were used to assess the relationship between activations and the behavioral tests. Areas of statistical significance were identified using a height and extent threshold of p < .05, corrected for the number of comparisons. To characterize the correlations, the significant regions were treated as ROIs. To visualize the relationship, the contrast values for each ROI were extracted and plotted against behavioral scores. In addition, the individual beta weights for route and survey learning were extracted to determine whether one or both encoding conditions appeared to be changing as a function of the behavioral tests.

Results

Behavioral Results

Recognition and map drawing results for these participants have been reported previously (Shelton & Gabrieli, 2002) and revealed no overall differences in accuracy for route and survey learning. Means (standard deviations) for the three spatial skill tests were 20.67 (4.14), 16.67 (4.23), and 154.92 (15.91) for the MRT, the RMT, and the PT, respectively. Despite obtaining an adequate range of scores on all three spatial skill tests, none of them correlated with recognition or map drawing performances (p > .2 for all rs). Among the spatial skill tests, all simple correlation analyses were significant: MRT was positively correlated with RMT (r = .82, p = .001) and PT (r = .88, p < .001), and RMT and PT were positively correlated (r = .67, p = .02).

Brain Activation

Overall group differences between route and survey encoding and between each type of encoding and the fixation baseline were

1 Examples of the types of movies used in this study can also be found at www.psy.jhu.edu/~ashelton/stimuli.

2 This test is the same one used by Pazzaglia and De Beni (2001) to demonstrate the relationship to strategy.
presented in a previous article (Shelton & Gabrieli, 2002) and summarized in the introduction and Figure 1.

Because of the strong positive relationships among the spatial skill measures and the primary interest in mental rotation as a predictor, the analyses focus on the correlation between brain activation and MRT score. (Analyses were repeated with the RMT scores, the PT scores, and a composite score. All revealed largely similar results.) First, the activation for the route versus survey contrast in the ROIs from the direct comparison was correlated with MRT scores. The only region to reach statistical significance was the anterior portion of the parietal cortex (postcentral gyrus, BA 5/7). Details on the activation in this region are provided in the whole-brain analysis that follows.

To assess the degree to which route versus survey differences were mediated by MRT score, we correlated the contrast images for the difference between route and survey encoding with MRT scores by using a simple linear regression. As shown in Figure 3 (top), significant areas of activation were observed in the right and left middle frontal gyrus (BA 9 and inferior 6), an area of the left cingulate cortex (BA 24), and the right and left superior parietal cortices (postcentral gyrus/precuneus, BA 5 and 7). In all of these regions, better mental rotation ability was associated with greater activation for route than for survey (Figure 3, middle). No regions showed the opposite correlation, even at liberal thresholds. A color version of Figure 3 is on the Web at http://dx.doi.org/10.1037/0894-4105.18.3.442.supp.

The observed correlation could be due to increased activation during route encoding or to decreased activation during survey encoding for individuals with better mental rotation skills. To test these alternatives, we extracted the signal change for route and

Figure 3. Top: Brain activation for route minus survey activation correlated with the Mental Rotation Test (MRT; Vandenberg & Kuse, 1978) score. All outlined regions reflect positive correlations. Middle: Correlation between MRT score and route minus survey activation in each region of interest (ROI). Bottom: Correlation between MRT score and activation for route minus fixation and survey minus fixation in each ROI. Left and right ROIs were collapsed for presentation. A color version of this figure is available on the Web at http://dx.doi.org/10.1037/0894-4105.18.3.442.supp.
survey relative to baseline separately in each of these ROIs and correlated each participant’s activation with his or her MRT score. When interrogated this way, all regions showed little or no correlation between route encoding and MRT score and significant negative correlation between survey encoding and MRT score (Figure 3, bottom), suggesting that the correlation is due to differential recruitment during survey encoding. To further support these findings, the correlations were also analyzed in the whole brain at liberal thresholds. The results were consistent with the previous analysis showing the same ROIs for survey minus fixation but not for route minus fixation. No other regions appeared to be correlated with spatial abilities.

Postexperiment interview responses were also examined in the context of the observed correlations. With regard to the ease of route and survey learning, 5 out of 6 of the participants with the greatest activation for survey minus fixation in the observed ROIs reported more difficulty with the survey environment than the route environment (1 reported that they were equally difficult). The remaining 6 participants generally reported that they were equally difficult (4) or that route was slightly harder (2). The relationship between the activation and self-reported difficulty was significant, \( \chi^2(2, N = 12) = 8.8, p = .012 \). With regard to facility with maps, the 4 participants with the greatest activation for survey minus fixation reported difficulty in dealing with maps and a tendency to turn maps to match their orientation. The 4 participants with the least activation in this contrast reported facility with maps and no need for turning or reorienting. The remaining 4 participants had mixed responses to the self-report questions. This relationship was marginally significant, \( \chi^2(1, N = 12) = 3.1, p = .078 \).

**Discussion**

Mental rotation skill was associated with individual differences in subjective difficulty for learning survey spatial information and with individual differences in brain activation during survey learning. In specific frontal, anterior cingulate, and parietal regions, there was a strong positive correlation between the activation for route versus survey encoding and mental rotation ability. This activation change as a function of spatial skill appeared to be specific to the survey encoding, with decreased recruitment of these brain regions during survey encoding (relative to fixation) as mental rotation score increased.

Individual differences are generally studied in tasks that show how performance is affected by skill. However, one difficulty in examining spatial skill differences in the context of large-scale spatial learning is the realization that different strategies can lead to successful performance (Denis et al., 1999; Passini, 1984). In the present study, behavioral performance did not vary as a function of the particular spatial skills tested; however, the self-reports were consistent with different preferences. For example, participants with lower mental rotation scores (i.e., those with greater survey-fixation activation) reported greater difficulty for survey than for route encoding. Participants with higher mental rotation scores did not report this difficulty, suggesting that they were able to use strategies that were less taxing than those used by participants with lower mental rotation scores.

The apparent relation between mental rotation performance and survey encoding is consistent with previous behavioral data showing a relationship between preference for survey information and mental rotation (Pazzaglia & De Beni, 2001). That this relationship is characterized by a decrease in the activation of certain regions as mental rotation skill improves suggests that these regions may be associated with processes that are used more efficiently for survey or map learning because of superior mental rotation abilities. On the basis of previous findings in these brain regions, we considered what those processes might entail.

The anterior cingulate cortex has been associated with executive functions such as error monitoring and response conflict (Carter et al., 1998; Dehaene, Posner, & Tucker, 1994; Gabriel, Burhans, Talk, & Scafl, 2002; Luu, Tucker, Derryberry, Reed, & Poulsen, 2003; Posner & DiGirolamo, 1988). In the present study, the activation in this region associated with survey learning in participants with poorer mental rotation skills may reflect the difficulty these individuals may have had with the survey encoding. For example, when a participant is less comfortable with the encoding condition, he or she may engage in greater degrees of self-monitoring, a sort of checking and rechecking of the encoding processes to determine whether the information is being adequately laid down. Such an explanation would be consistent with subject reports showing that participants with the greatest activation during survey encoding relative to fixation reported that survey encoding was more difficult than route encoding.

The functional organization of the prefrontal cortex is a matter of much debate (e.g., Fuster, 1989; Stuss & Knight, 2002); however, it is widely accepted that regions of prefrontal cortex participate in working memory and attentional processes (e.g., Cohen et al., 1997; Courtney, Ungerleider, Keil, & Haxby, 1997; Goldman-Rakic, 1984, 1996; Haxby, Petit, Ungerleider, & Courtney, 2000; Levy & Goldman-Rakic, 1999). The decrease in this region for survey encoding as a function of MRT score suggests that participants with better mental rotation ability require less of these attentional and/or working memory resources during survey encoding. This would be consistent with the interpretation of the anterior cingulate activation, suggesting that mental rotation ability may allow simplified strategies for encoding from the survey perspective.

The observed parietal activation (postcentral gyrus/precuneus) would also be consistent with an attentional explanation given the established role of both frontal and parietal cortices in the control of attention (e.g., Corbetta & Shulman, 2002; Knight, 1997; Mesulam, 1990, 1998; Posner & Petersen, 1990). However, parietal regions, and the intraparietal sulcus (BA 7) in particular, have also been closely associated with attention to and representation of spatial information. More specifically, the parietal cortex has been associated with representing space in egocentric (observer-centered) reference frames (e.g., Andersen et al., 1997; Colby & Goldberg, 1999; Halligan, Fink, Marshall, & Vallar, 2003; Robertson & Marshall, 1993). Moreover, the region correlated with MRT score overlaps with the region identified with route encoding independent of spatial skill (Shelton & Gabrieli, 2002), suggesting that it is preferentially recruited for route encoding in general but becomes increasingly recruited for survey encoding as mental rotation skill declines across individuals.

One interpretation of the parietal participation is that participants with weaker mental rotation skills relied on egocentric processing for both route and survey encoding, whereas participants with stronger mental rotation skills were better able to capitalize on the structure of the survey perspective without ap-
pealing to the egocentric properties of an environment. For example, a participant with stronger mental rotation skills may learn the environment as a map without regard for how navigation in the environment might proceed, whereas a participant with weaker mental rotation skills may need to think about being in the environment to understand the layout. Support for this interpretation comes from the postexperiment interviews, which indicated that participants with the greatest activation for survey encoding relative to fixation reported more difficulty with map learning and a tendency to turn maps to match their own orientation.

The egocentric processing explanation suggests that participants might differ in the degree to which they rely on egocentric transformation of space. The battery of tests we used with our participants was designed to differentiate egocentric transformations from object-based transformations. Although we were unable to distinguish participants on these two types of transformations in our small sample (because of correlations among our tests), previous research has shown them to be both behaviorally (Zacks, Mires, Tversky, & Hazeltine, 2000) and neurologically (Zacks, Rypma, Gabrieli, Tversky, & Glover, 1999) dissociable. Whether this dissociation can be used to assess the source of individual differences remains an empirical question, but the present results suggest that identifying individuals with different strengths may provide additional insights into how information is processed differently.

One concern with the absence of correlation between mental rotation and the route-fixation contrast is the restriction of range, which limits the ability to find significant correlation. As seen in Figure 3 (bottom), activation values for route encoding relative to fixation had smaller ranges than that for survey encoding. However, this restriction of range is unlikely to lead to the conclusion that mental rotation is associated more with differential recruitment during survey encoding. First, given that these correlation analyses are in the same individuals (and relative to the same fixation baseline), the difference in range provides additional support for the claim that survey encoding is showing a greater degree of differential activation across participants than route encoding. Indeed, relative to fixation, survey encoding is more variable than route encoding and that variability is reliably associated with mental rotation score assessed outside of the scanner. In other words, given the prior literature that mental rotation skill is associated with survey preference but not route preference, it would be expected that activations associated with mental rotation skill would show survey-related variation but not route-related variation.

Second, other regions of the brain showed equal or greater variance for the route encoding compared with the survey encoding. For example, all of the regions used in the ROI analysis show roughly equal variance for route and survey encoding relative to fixation (see Shelton & Gabrieli, 2002). In the two parietal regions that showed significant correlation with MRT score, the variances are equal when the larger ROI is used in the analysis. Even with equal variances, the correlation is driven by significant changes in survey but not route encoding as a function of MRT score. Therefore, it is not the case that there was in general less activation variance for route encoding and, therefore, less opportunity for a correlation with route activation to be observed. Rather, the variation in route activation was similar, overall, to that for survey activation, but the variation in route activation did not correlate with mental rotation ability.

In the present study, there was no relation between behavioral measures of mental rotation ability and memory for survey displays (although there was a relation between mental rotation ability and self-reports of the difficulty of learning survey information in the experiment and in life). This lack of a behavioral correlation occurred despite the finding that greater mental rotation ability was associated with less activation for survey learning. It may be that differences in survey-learning ability were obscured by overlearning (i.e., ceiling scores), because participants saw each survey environment seven times and were over 95% accurate in recognition memory. By this view, such a behavioral relation may be observable after fewer exposures to the environment. Indeed, behavioral work on self-terminated learning has shown that, with fewer exposures, the accuracy with which participants can build models of learned environments (a survey-like task) differs following route and survey encoding and improves as mental rotation score increases (Shelton & Clark, 2003). Although these data come from a retrieval task, they suggest that a more direct examination of survey encoding with limited exposures might reveal a correlation between performance and mental rotation scores. Alternatively, the learning situation used in the present study may have been amenable to various spatial learning strategies. In functional neuroimaging, magnitudes of activation are often related to individual differences in performance (e.g., for spatial skills, Hartley, Maguire, Spiers, & Burgess, 2003; Shelton, Christoff, Burrows, & Gabrieli, 2003). Such studies have the advantage of directly relating variation in activation to variation in performance, but they have the disadvantage of confounds between performance and activation. For example, activation differences may reflect slower processing or more errors or even frustration with a task. In that sense, it is unclear if the activation differences reflect the brain basis of the cause of individual differences or the consequences of individual differences. The equal survey spatial learning of individuals with better or worse mental rotation skills indicates that the present results cannot simply be accounted for by the consequences of individual differences in task performance. At the same time, the lack of a direct relation between activation and survey spatial learning makes uncertain the relation between these neural systems and variation in survey spatial performance.

It is clear from the present study that successful learning occurred in individuals who differed on spatial skills (previously associated with preferences) and on their comfort level with the different types of encoding. In the brain, the differences in activation as a function of mental rotation can best be characterized as reflecting differences in the way the information is processed, suggesting alternative strategies for learning. Future research is required to elucidate the degree to which successful performance is directly dependent on these proposed strategic differences. For example, the current interpretation would predict that spatial learning tasks that do not permit alternative strategies would result in poorer survey or map learning for those individuals with lower mental rotation scores. Similarly, these results might predict that mental rotation training might alter the strategies (i.e., brain processes) used in survey encoding. In the brain, such transfer of training would predict a difference in activation for survey encoding pre- and posttraining.
Despite these unanswered questions, the present study suggests that brain imaging can reveal processing differences, linked to domain-specific abilities, associated with similar performance. Although we have taken only the initial steps, understanding multiple mechanisms for achieving successful performance opens the door to investigating how different strategies might work and whether they can be invoked when problems arise such as brain injury.

References


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