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Joint angles and angular velocities and relevance of eigenvectors during prehension in the monkey

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Abstract

Hand shaping during prehension involves intricate coordination of a complex system of bones, joints, and muscles. It is widely hypothesized that the motor system uses strategies to reduce the degrees of independent control. Both biomechanical constraints that result in coupling of the fingers and joints and neural synergies act to simplify the control problem. Synergies in hand shaping are typically defined using principal component-like analyses to define orthogonal patterns of movement. Although much less examined, joint angle velocities are also important parameters governing prehension. The primary goal of this study was to evaluate joint angles and joint angle velocities during prehension in monkeys. Fourteen joint angles and angular velocities were measured as monkeys reached to and grasped a set of objects designed to systematically vary hand shapes. Hand shaping patterns in joint angles and velocities were examined using singular value decomposition (SVD). Highly correlated patterns of movements were observed in both joint angles and joint angle velocities, but there was little correlation between the two, suggesting that velocities are controlled separately. Joint angles and velocities can be defined by a small number of eigenvectors by SVD. The unresolved question of the functional relevance of higher-order eigenvectors was also evaluated. Results support that higher-order components are not easily distinguished from noise and are likely not of physiological significance.

Keywords

Reach to grasp; Joint angles; Angular velocities; Hand shaping; Principal components; Synergy

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Introduction

The ability of humans and non-human primates to make intricate hand movements is a function of its biomechanical complexity (MacKenzie and Iberall 1994). A fundamental question is how the central nervous system controls the hand in tasks such as prehension (MacKenzie and Iberall 1994). Many studies support that the motor system simplifies the control problem by reducing the large number of degrees of freedom. In both humans and monkeys, grasping objects involves correlated motions of multiple joints (Mason et al. 2001, 2004; Santello et al. 2002; Santello and Soechting 1998) that occur in a host of hand movements (Soechting and Flanders 1997; Engel et al. 1997; Jerde et al. 2003a; Thakur et al. 2008). Similarly, anatomy introduces biomechanical constraints and coupling of joints that reduce the level of individual control (Schieber 1991, 1995; Schieber et al. 1997; Tubiana 1981; Schieber and Santello 2004).

Authors have suggested that the neural control strategy for the hand involves synergies [for reviews, see (Santello et al. 2013; Schieber and Santello 2004)]. Synergies specify patterns in joint movements during complex motions as defined by joint kinematics, forces, or muscle activation (Saltzman 1979). Hand synergies based primarily on joint angles have been defined for many tasks, including static hand postures (Jerde et al. 2003b; Santello et al. 1998), reaching and grasping objects (Braidó and Zhang 2004; Mason et al. 2001, 2004; Theverapperuma et al. 2005), and unconstrained movements (Thakur et al. 2008; Ingram et al. 2008). Extensive covariation of joint angles during opening of the hand is one dominant hand shape consistently demonstrated by humans and non-human primates (Santello et al. 1998; Santello and Soechting 1998; Theverapperuma et al. 2005). Additional hand shaping patterns have not been consistent across studies.

Speed of the arm, hand, and fingers during prehension is important for proper timing, yet few studies have examined the speed of finger joint angles during grasping or hand shaping. An early study found that joint angles and fingertip trajectories were highly variable during a rapid precision task, but joint angular velocities were relatively constant across trials and had bell-shaped profiles (Cole and Abbs 1986). This study had minimal task variation and started with the hand fully open. In contrast, Vinjamuri et al. described joint angular velocities as increasing at the start of prehension, followed by a decrease to a negative velocity and a return to zero (Vinjamuri et al. 2007, 2009). Variability of joint angular velocities during prehension has not been well studied nor has their relationship with joint angle movement. Few studies have defined hand shaping synergies based on joint angular velocities in humans (Ingram et al. 2008; Vinjamuri et al. 2007, 2009). To our knowledge, no study of hand motion synergies has used angular velocities in non-human primates.

Synergies are often defined using principal component analysis (PCA) or similar techniques to identify orthogonal patterns and reduce a complex system's degrees of freedom. A large variety of grasp shapes can be described by scaling a few “global” eigenvectors (EVs) with large eigenvalues as defined by principal components (PCs) or EVs (Mason et al. 2001, 2004; Santello et al. 1998; Theverapperuma et al. 2005). What EVs with small eigenvalues capture is not clear, but it has been suggested that these higher-order EVs are needed to fully reconstruct detailed hand motion (Santello et al. 1998; Thakur et al. 2008). From a statistical

viewpoint, EVs with eigenvalues equal to or less than that of random data are likely driven by noise or outliers in the data and can be ignored (Freund and Littel 2000; Jackson 2003; Jolliffe 2002; Duntzman 1989). By definition, singular value decomposition (SVD) applied to completely random data will result in n eigenvectors, each with an eigenvalue of $1/n$, where n is the number of components input to the system. To date, no studies have examined the proper number of synergies to use when reconstructing joint angles and angular velocities of the primate hand.

This paper examines 14 joint angles and angular velocities as two Rhesus monkeys reached to and grasped a set of 23 objects. Covariation among joint angles and velocities was examined. Hand shaping patterns were studied using SVD, a form of PCA that also identifies the vector scalings of the system (Jackson 2003; Jolliffe 2002). The eigenvalues for each EV and the reconstruction error (RE) were examined to determine the number of relevant EVs.

Materials and methods

Behavioral task

The experimental protocol was approved and monitored by the University of Minnesota Institutional Animal Care and Use Committee and conformed to the “Guiding Principles in the Care and Use of Animals” of the American Physiological Society.

Two head-fixed Rhesus monkeys (*Macaca mulatta*; monkeys S-6 kg and B-5 kg) were trained to reach and grasp a set of objects using a power grasp. The animals were secured in a chair and viewed a computer monitor (45 cm in front) (Fig. 1a). The forearm of the reaching arm was in a neutral position; the volar surfaces of the fingers in opposition to the palm and thumb were used to grasp the object. The non-task arm was gently restrained. A start pad was located anterior (3 cm) and lateral (10 cm) to the animal's midline. An object with embedded force sensors was located directly in front of the animal at mid-chest level. The reach distance from the start pad to the object was approximately 15 cm. Objects were secured to a base to prevent rotation or translation of the object during grasp.

To begin a trial, the monkey placed its hand on the start pad (flat plate with force sensor), turning on the screen (Fig. 1a, b). After a variable delay, a visual instructional cue (red bar) appeared on the computer screen indicating the required grasp force level (upper left—premove epoch). During the premove epoch (random duration 1–1.5 s), the animal was required to hold the start pad until a go cue (green cursor) signaled the monkey to initiate reach (upper right—reach epoch). The monkey then moved its hand from the start pad to the object and was required to obtain a static grasp force of 0.5 N (± 0.1 N) within 500 ms and maintain that force (2–4 s) through whole-hand grasping of the object. Monkeys were required to complete the reach within 2 s of the “go” cue, but no constraints were made on either the speed of movement or the exact hand shape so that movements could be as natural as possible. When the cues disappeared, the monkey returned its hand to the start pad (~ 1 s) before receiving a juice reward (lower left, end of trial/next trial). Objects were randomly selected and presented in blocks of 5 (monkey B) or 10 (monkey S) repetitions per block. We acknowledge that control over grasp force is not perfect and there remained some

variability in grasp force that could affect hand posture. However, because we performed all analysis trial by trial with no averaging and the paradigm allowed minimal variation in grasp force, we feel that the current analysis is sufficient to discuss hand shaping without incorporating grasp force effects.

A set of 23 objects (Fig. 1c) was designed to create a large systematic variation in hand shape during a lateral grasp. Objects were precision-machined from aluminum with force sensors embedded beneath the surface. To ensure a lateral rather than overhand grasp, the manner in which force was applied to the objects was tightly controlled. Most objects contained two vertically embedded force sensors (Force Sensing Resistors®, Interlink Electronics©, Camarillo, CA) located on opposite sides of each object, approximately where lateral forces were applied with the finger pads and palm. Three narrow-width objects (1, 6, and 7) allowed for placement of only one sensor. The paradigm required force to be applied to both sensors if two were present.

Behavioral data collection and processing

Fingers, hand, and wrist kinematics were monitored in three dimensions using a 6-camera video motion capture system [Motion Analysis Corp. (MAC), Santa Rosa, CA], and 17 passive reflective markers glued to the monkey's shaved hand. The video signal was digitized at 120 Hz and processed offline (EVaRT software, MAC). Analog data from the object and start pad were simultaneously recorded with the kinematics to properly identify epochs within trials. Reflective markers were constructed by covering 2-mm-diameter plastic spheres with reflective tape. One marker was placed proximal to the dorsal wrist crease and at the dorsal wrist crease, thumb carpometacarpal joint and thumb metacarpophalangeal (MCP) and interphalangeal (IP) joints, and near each long-finger MCP joint, proximal IP joint and distal IP joint.

Fourteen joint angles [thumb metacarpophalangeal (THMCP), MCP angles for digits 2–5 (MCP2–5), proximal IP for digits 2–5 (IP2–5), adduction/abduction 1–4 (ABD1–4), and wrist flexion/extension (WFLEX)] were determined. Joint angles were defined by vectors drawn between markers. For example, the MCP joint angle of the middle finger was defined as the angle between the vector drawn from the marker at MCP3 and the wrist crease and the vector from MCP3 to IP3. Joint angular velocities (JAVs) were derived from joint angles (JAs) in equal time steps (8.33 ms). JAs and JAVs were filtered using an 83.3-ms sliding average filter. JAs were adjusted using an experimentally derived relationship to compensate for marker offsets from actual joint centers prior to deriving JAVs and filtering.

Data analysis

The data were divided into three epochs: premove, reach, and grasp. Reach onset was defined as the time at which the change in force on the start pad first dropped below 10 N/s. Grasp onset was defined as the time at which the change in force on the object first exceeded 10 N/s. All data were aligned on grasp onset. The premove epoch was defined as the 250 ms before reach onset and the grasp epoch as the 250 ms after grasp onset. The reach epoch was the time between reach initiation and grasp onset (~400 ms). The ranges in JA and JAV

during *remove*, at three specific time points during *reach* (100, 200, and 300 ms), and *grasp* were examined to evaluate variation in hand shaping across all trials within a session.

Colinearity that exists between kinematics was quantified. The correlation coefficient for the entire temporal progression of the JAs and JAVs was calculated between each pair of elements for each session separately and averaged across sessions.

SVD was performed for all trials in each session using the 14 JAs and JAVs (separately) to identify patterns in hand shaping and define orthogonal data components. SVD is similar to PCA as it identifies patterns and uncorrelated components (or eigenvectors), but SVD also provides the temporal scaling of the patterns (Jackson 2003; Jolliffe 2002). SVD was performed by first constructing the data (X) matrix:

$$X = \begin{bmatrix} p_1(\text{trial}_1, \text{time}_1) & p_2(\text{trial}_1, \text{time}_1) & \dots & p_n(\text{trial}_1, \text{time}_1) \\ p_1(\text{trial}_1, \text{time}_2) & p_2(\text{trial}_1, \text{time}_2) & \dots & p_n(\text{trial}_1, \text{time}_2) \\ \dots & \dots & \dots & \dots \\ p_1(\text{trial}_1, \text{time}_t) & p_2(\text{trial}_1, \text{time}_t) & \dots & p_n(\text{trial}_1, \text{time}_t) \\ p_1(\text{trial}_2, \text{time}_1) & p_2(\text{trial}_2, \text{time}_1) & \dots & p_n(\text{trial}_2, \text{time}_1) \\ p_1(\text{trial}_2, \text{time}_2) & p_2(\text{trial}_2, \text{time}_2) & \dots & p_n(\text{trial}_2, \text{time}_2) \\ \dots & \dots & \dots & \dots \\ p_1(\text{trial}_i, \text{time}_t) & p_2(\text{trial}_i, \text{time}_t) & \dots & p_n(\text{trial}_i, \text{time}_t) \end{bmatrix}$$

where i is the number of trials, t is the number of time bins, and n is the number of parameters [JAs or JAVs (p)] being used in the analysis. *Premove* (250 ms), *grasp* (250 ms), and the entire *reach* (~400 ms) were used in the analysis. Joint angles and JAVs were standardized by first subtracting the mean and then dividing by the standard deviation of each element to eliminate arbitrary weights due to differences in magnitude of elements (Santello et al. 1998; Jolliffe 2002). Matrix X was decomposed into three matrices using $X = U\Sigma V^T$. Matrix U contained the coefficients describing each individual element's contribution to the EV. The matrix V contained the vector scaling explaining the involvement of each EV over the course of time. The superscript T indicates the transpose of the matrix. Matrix Σ contained the eigenvalues, or the amount of variance described by each EV. For each parameter across all time bins and trials within a session, the data were randomized using MATLAB's "rand" command. This produced a randomized set of data with the same statistics as the original data, to examine the eigenvalues obtained from this randomized data.

To assess the number of EVs required to accurately reproduce actual hand shapes, the RE was calculated (Vinjamuri et al. 2009). First, the reconstructed JA or JAV values were calculated with each possible number of eigenvectors (1–14) for each session. RE was then obtained by using the equation

$$\text{RE} = \frac{\sum_{n=1}^N \sum_{t=1}^T [p_n(t) - \hat{p}_n(t)]^2}{\sum_{n=1}^N \sum_{t=1}^T p_n(t)^2}$$

in which $\hat{p}_n(t)$ is the profile of the reconstructed parameter being examined (JA or JAV) at time t at each joint n , and $p_n(t)$ is the actual parameter. The RE was determined using two methods. Because we used standardized data for the SVD analysis in the first method, the average JAs or JAVs were not added back into the data for reconstruction. The second method added the average JAs and JAVs back prior to reconstruction. These two methods provided an estimate of the reconstruction with and without including the large variance explained by the average JAs or JAVs.

Results

Joint angles and velocities during prehension

Analysis was based on 43 complete experimental sessions from Monkey S and 10 sessions from Monkey B (approximately 100–400 trials per session). Reach durations were generally brief (399 ± 33 ms for monkey S and 443 ± 19 ms for monkey B) with little variability over a fixed distance consistent with a ballistic strategy employed by both monkeys. Hand shaping during the task was described using JAs and JAVs for each digit and wrist flexion (THMCP, MCP2–5, IP2–5, ABD1–4, and WFLEX, see “Materials and methods” section) for the three epochs. The same model experimental session (from Monkey S) is used to demonstrate various analyses throughout the paper (Figs. 2, 3, 7). Population data are based on all sessions from both monkeys.

The temporal profile for each JA is shown across all epochs for the model session in Fig. 2. JAs increased through the first half of reach as the hand opened. Shaping of the hand continued through the second half of reach when JAs decreased as the hand approached and enclosed the object. This temporal progression of hand shaping is typical of previous observations in human and non-human primates (Jeannerod 1984; Mason et al. 2001; Roy et al. 2000; Santello and Soechting 1998; Hu et al. 2005) and demonstrates a similar pattern of movement in a large number of finger joints. Finger abduction followed a different pattern as ABD1–2 JAs decreased initially after movement onset and then increased as the hand approached the object. In contrast, ABD3 generally decreased throughout reach, but had little overall change. ABD4 decreased as well, but included a small increase midway through reach (Fig. 2c). IP5 (extension/flexion of the second joint of the little finger) and ABD4 (abduction of small finger) displayed a temporal progression less stereotypical across trials than other JAs, similar to findings in humans that the little finger is less involved with hand shaping (Ansuini et al. 2006).

Most previous studies of finger movements during grasping only examined joint angles (Santello and Soechting 1998; Mason et al. 2004) or grasp aperture (Chieffi and Gentilucci 1993; Jeannerod 1981; Paulignan et al. 1991). Finger JAVs in non-human primates have not been thoroughly studied (Braido and Zhang 2004; Mon-Williams and Tresilian 2001; Zhang et al. 1998). Because velocity in motor control is important for timing, JAVs were also evaluated. For the model session, THMCP, MCP2–5 (Fig. 3a), IP2–5 (Fig. 3b), and WFLEX (Fig. 3c), JAVs increased initially after movement onset during hand opening and then decreased through peak aperture as the hand approached the object (Vinjamuri et al. 2007). The angular velocities of ABD1–4 also displayed a similar biphasic profile (Fig. 3c).

Variability in joint angles and velocities

Joint angles were tightly clustered for trials until midway through reach after which the angles diverged to accomplish different grasp shapes (Santello et al. 1998; Theverapperuma et al. 2005; Mason et al. 2001, 2004). The average range in JAs within a session increased throughout *reach* and was maximal during *grasp* (Fig. 4a, b). Large ranges in JAs during *grasp* display the variability in hand shaping elicited by the object set. The progression of variability exemplifies the preshaping to objects that occurs during prehension (Mason et al. 2001, 2004; Jeannerod 1984; Roy et al. 2000; Santello and Soechting 1998; Hu et al. 2005; Santello et al. 2002; Thakur et al. 2008). As required by the task, JAVs were approximately zero during *remove* when the hand was on the start pad and during *grasp* after the hand reached its final posture (~100 ms after grasp onset), but exhibited much greater variability during *reach*. Variability in JAVs was maximum midway through reach (Fig. 4c, d). In contrast with a previous study (Cole and Abbs 1986), JAVs vary markedly with grasp shape.

Correlations among joint angles and velocities

To examine the colinearity in the data, the correlation coefficient for each possible pair of JAs and JAVs was calculated across all epochs and averaged across sessions (Fig. 5). Many of the JAs were highly correlated (Fig. 5a). MCP2–5 and IP2–5 JAs were strongly and positively correlated ($r > 0.5$), as observed in human grasp (Schieber 1991; Soechting and Flanders 1997). The THMCP angle was less strongly correlated with the MCPs and IPs (0.3–0.5) and had the lowest correlation with MCP2, indicative of independent control of the thumb relative to the long fingers (Schieber 1991; Soechting and Flanders 1997). ABD4 was positively correlated with the MCPs, IPs, and WFLEX, although overall had the lowest correlations with all JAs, consistent with the independence often found in the little finger (Ansuini et al. 2006). JAVs displayed similar correlations with the highest positive correlations among the MCPs, IPs, and WFLEX (Fig. 5b). JAs and JAVs had little correlation ($-0.25 < r < 0.28$) consistent with these measures being orthogonal (Fig. 5c). Therefore, groups of highly correlated joint motions exist across this diverse set of objects.

Eigenvector analysis

Coefficients for the JAs in each of the first 5 EVs for the model session for both JA and JAV SVDs are shown in Fig. 6. Explaining 29 % of the variance, EV1 described opening and closing of the hand through a coordinated increase of MCP and IP angles, ABD3–4, and WFLEX. EV1 also included a decrease in ABD1 and ABD2. This EV can be appreciated in both the model session (Fig. 6a) as well as all sessions (Fig. 6b). EV2 explained 13 % of the variance and was weighted toward an increase in IP joints, a decrease in ABD3, and a smaller decrease in MCPs (Fig. 6a). EV3 captured a decrease in THMCP and increase in MCP2 and ABD2, representing the pattern of individuation often observed with the forefinger (Schieber 1991; Soechting and Flanders 1997). EV4 was highly weighted for the decrease in ABD1–4 and had an eigenvalue (9 %) close to EV3. The remaining EVs described additional details of hand shaping.

EV1 based on JAVs had negative weightings similar in magnitude for THMCP, MCP2–5, IP2–5, ABD4, and WFLEX (Fig. 6c) and had an eigenvalue of 29 %. EV2 explained 11 % of the variance and was dominated by an increase in the JAV of ABD3, but also contained

positive weightings for the JAV of MCP2–5 and negative weightings for the JAVs of IP2–5. EV3 was mainly positively weighted for ABD4 and negatively for THMCP JAVs.

For both JAs and JAVs, EV1 had small standard deviations across sessions (Fig. 6b, d), displaying a consistency in coefficient patterning, while higher-order EVs generally had larger variability. The average dot product between EV1 of each session was 0.94 (max of 1 for two eigenvectors) for both monkeys (values in upper left of Fig. 6b, d) and ranged from 0.61 to 0.77 for EVs 2–5. This supports the observation that the first eigenvector had more consistent patterning than the remaining eigenvectors.

SVD analysis demonstrates that approximately 25 % of the variance was explained by the first EV for both JAs (25.2 ± 4.3 %) and JAVs (25.9 ± 3.6 %) (Fig. 7a, b). The first 5 EVs explain a total of 65.5 ± 4.2 % of variance for JAs and 65.2 ± 3.7 % for JAVs. These values are lower than those found in previous studies (Braido and Zhang 2004; Mason et al. 2001, 2004; Santello et al. 1998; Thakur et al. 2008) because all time bins for each trial were used in analysis without averaging, increasing trial-to-trial variability. Furthermore, as detailed in the “Materials and methods” section, the SVD analysis was standardized, and therefore, the mean hand shape removed. If included in the analysis, the average hand shape will explain a large fraction of the variance.

An important question is the significance of higher-order EVs. By definition, SVD analysis results in higher-order EVs that explain some of the variability and can be used to improve reconstruction of the original data set. Whether this is physiologically meaningful was examined in two ways. First, SVD analysis of randomized data resulted in eigenvalues of 7.14 % (1/14th of 100 %) for each EV, suggesting that EVs with lower eigenvalues capture insignificant patterns or noise in the data (Fig. 7a, b, dashed line). Only 4–5 EVs, those with eigenvalues >7 , likely represent biologically relevant patterns in hand shaping.

The second approach evaluated the quality of the reconstruction. We analyzed RE using two approaches (see “Materials and methods” section). First, using the standardized data (“Stand”) to compute the SVD in which the average JAs or JAVs are removed (as done throughout the analysis) and not included in the RE (Fig. 7c, d, black circles). The second approach (“Non-Stand”) added the average hand shape into the RE (Fig. 7c, d, white circles). As shown in previous studies, the first PC or EV essentially represents the average hand shape and can account for a major fraction of the hand shape variability (Santello et al. 1998; Mason et al. 2001; Thakur et al. 2008). Calculation of the RE in each session, including the average JA, reveals that using only a single EV from JAs is sufficient to accurately reproduce the data ($RE = 0.10$) (Vinjamuri et al. 2009). The average RE for the population for one EV was only 0.004 ± 0.005 (Fig. 7c). Reconstruction of JAVs with the average JAV required 5 EVs to accurately reproduce the data (Fig. 7d), similar to previous findings (Vinjamuri et al. 2009). If the average JA or JAV is not included, it requires 6 EVs to reach an RE of 0.10. Therefore, the initial 6 EVs are likely biologically relevant and useful in reconstruction, while the physiological significance of higher-order EVs remains highly questionable.

Discussion

During prehension, humans and non-human primates preshape the hand to match properties of the object to be grasped (Jeannerod 1984; Paulignan et al. 1991; Castiello et al. 1993, 1998; Mason et al. 2004; Roy et al. 2002; Wing et al. 1986; Santello and Soechting 1998). Earlier studies established that preshaping begins approximately midway through reach (Mason et al. 2004; Santello and Soechting 1998). Confirming early observations, JAs were generally the same across trials during *remove* and the first part of *reach* and began to diverge at the end of *reach* (Fig. 2). The largest differences in the JAs occurred during *grasp* (Fig. 4a, b). This evolution in JAs across epochs is explained by preshaping and final grasp shaping for a highly varied set of objects. The IP5 and ABD4 JAs displayed a much less consistent progression with time, suggesting less involvement with preshaping of the hand for grasp.

JAVs have been less studied. Most joints (THMCP, MCP2–5, IP2–5, and WFLEX) followed a pattern of a rapid increase in angular velocity followed by a long decrease in velocity through peak aperture (Fig. 3). This is consistent with a strategy of quickly opening the hand to maximum aperture and then slowing before contact and final hand shape (Vinjamuri et al. 2007, 2009). Similar to JA progressions, IP5 and ABD4 JAVs displayed a much less consistent pattern in time. Overall, JAV variability increased during *reach* (Fig. 4c, d) as the hand was shaping.

One main goal in examining kinematics of hand shaping is to better understand how the central nervous system controls this complex apparatus. During prehension in humans, there is a high level of colinearity between JAs (Braido and Zhang 2004; Mason et al. 2001; Thakur et al. 2008; Santello et al. 2002; Santello and Soechting 1998). Biomechanical constraints within the hand, neural control, and the nature of the task are all likely to contribute. In this study, MCP and IP joint angles were highly positively correlated with each other, as well as with wrist extension (Fig. 5). These JAs change synchronously in time as the hand opens and then closes around the object (Theverapperuma et al. 2005). Other JAs are relatively independent or negatively correlated. Independence of ABD JAs with respect to MCP and IP JAs indicates that there may be separate neural mechanisms involved in control of these finger movements.

Similar results were observed for correlations between JAVs (Fig. 5). As expected, there is a lack of correlation between JAs and JAVs as these measures are orthogonal (Fig. 5). The inherent independence of position and velocity confounds the issue on whether the CNS independently controls these movement parameters. At a behavioral level, clearly, position and velocity can be independently controlled (Sing et al. 2009). Furthermore, single-unit recordings strongly suggest that the CNS can independently control position and velocity. Position and velocity coding has been described in the primary and premotor cortices, and for many cells, coding is independent (Wang et al. 2007; Paninski et al. 2004; Reina et al. 2001; Philip et al. 2013). Similar independent coding of position and velocity has been documented in the cerebellar cortex (Hewitt et al. 2011; Roitman et al. 2005). Examination of cortical and cerebellar firing with these parameters could help provide additional insight into control mechanisms. Furthermore, the high degree of correlation among many JAs and

among JAVs is a challenge for analysis of neural firing in relation to individual joint movements. One potential solution is to first extract a reduced set of independent patterns using PCA.

The first goal of SVD was to identify patterns of hand shaping. SVD resulted in a dominant hand shaping pattern in the first EV consistently identified throughout literature (Braido and Zhang 2004; Thakur et al. 2008; Mason et al. 2001; 2004; Santello et al. 1998). EV1 predominantly involved flexion/extension of the MCP and IP JAs, representing overall opening and closing of the hand (Fig. 6a). The remaining EVs captured differences in hand shaping across and within tasks. Higher-order EVs display large variability across studies of hand shaping in humans and non-human primates (Thakur et al. 2008; Mason et al. 2004; Ingram et al. 2008; Santello et al. 1998), which is quantitatively supported in this work (Fig. 6b). These differences have been interpreted as details in hand shaping (Santello et al. 1998; Thakur et al. 2008). Patterns in JAVs of the fingers during grasping have been described using a gradient descent algorithm (Vinjamuri et al. 2007), SVD (Vinjamuri et al. 2009), and PCA (Ingram et al. 2008), with results that do not easily compare with each other nor those found in the current study. Principal components obtained by Ingram et al. 2008 are most comparable to the EVs described here. Similar to JAs, EV1 obtained from SVD analysis of JAVs uncovers a dominant pattern highly weighted for the majority of MCP and IP JAVs (Fig. 6c) and is consistent across sessions (Fig. 6d). Because JAs and JAVs are independent (Fig. 5), SVD analysis of JAs and JAVs together is not discussed.

A second goal of SVD was to transform the data to a new coordinate system in which each component is independent. Due to the nature of prehension, biomechanical constraints, and neuroanatomy, many joint angles of the hand are highly correlated with one another. Colinearity is also present in this task (Fig. 5), particularly for JAs (THMCP, MCP2–5, IP2–5, and WFLEX) that make up the dominant hand shape. SVD transforms the data into a new coordinate system in which EVs are orthogonal (Jolliffe 2002; Jackson 2003; Tabachnick and Fidell 1996). By removing or minimizing elemental correlations using SVD, neural firing can be examined in relation to independent components rather than highly correlated individual elements, allowing for a better interpretation of the relationship.

SVD was used to reduce the degrees of freedom needed to explain a complex system. In this study, the hand was defined by 14 JAs or JAVs that were transformed into 14 orthogonal eigenvectors. Similar to previous findings, the first few eigenvectors explain the majority of the variance in hand shaping (Braido and Zhang 2004; Mason et al. 2001, 2004; Santello et al. 1998; Thakur et al. 2008). When attempting to reduce the degrees of freedom of a system, EVs describing less variance are often ignored because they are considered less important (Freund and Littel 2000; Jackson 2003; Jolliffe 2002; Duntzman 1989). The first 5 EVs, on average, had eigenvalues $>7\%$, the eigenvalue of randomized data (Fig. 7a, b) for both SVD of JAs and JAVs if one does not include the average hand shape or velocities. Eigenvectors with lower eigenvalues likely capture insignificant patterns or noise in the data, suggesting that only the first 5 EVs represent biologically relevant patterns in hand kinematics. The RE (Vinjamuri et al. 2009) based on the standardized data analysis also shows that ~ 6 EVs are needed to achieve an RE of $<10\%$. If the average JAs are included, the RE was dramatically lowered so that only a single EV was required to achieve adequate

reconstruction (0.10). Either methodology suggests that higher-order EVs are not necessary for reconstructing the details in hand shaping (Fig. 7c, d).

In conclusion, the results described here support previous findings that finger joint angles progress in a predictable manner as the hand opens to peak aperture and closes around an object (Jeannerod 1984; Paulignan et al. 1991; Castiello et al. 1993, 1998; Mason et al. 2004; Roy et al. 2002; Wing et al. 1986; Santello and Soechting 1998), suggesting a centralized control mechanism coordinates both amplitude and timing of these movements. Joint angular velocities, which have been less studied (Vinjamuri et al. 2007, 2009), show variability during reach, and implies that this parameter is important for controlled timing of the task. SVD results describe a dominant pattern in JAs in the literature (Braido and Zhang 2004; Thakur et al. 2008; Mason et al. 2001, 2004; Santello et al. 1998), but these results show a similar pattern in JAVs that had not been previously examined. Two methods support the conclusion that higher-order EVs resulting from SVD or other PCA types of analyses are not relevant or necessary for hand shape or velocity reconstruction. First, only 5 EVs had eigenvalues >7 %, supporting that higher-order EVs describe noise in the system. Second, the RE further emphasized that no more than 6 EVs were necessary to accurately reconstruct the data from the EVs. These results can be used to explore neural coding of detailed movements of the hand and can be applied to the development of more relevant and biologically accurate control algorithms for neuroprosthetics.

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Fig. 1. Apparatus and behavioral task. **a** Setup displaying position of monkey, start pad, object, and computer monitor. **b** Paradigm as viewed on screen by the monkey broken into epochs of the task. **c** Schematic of object set grouped in four series of which shape four is common to three. Example hands reproduced from actual kinematic data from a monkey are shown grasping representative objects

Fig. 2.

Plots of JAs in time for all trials in one session for Monkey S (objects 3–13, 15, 18–22). **a** MCP JAs for thumb (THMCP) and digits 2–5 (MCP2–5). **b** IP JAs for digits 2–5 (IP2–5). **c** Abduction/adduction angles between fingers (ABD1–4) and wrist flexion/extension angle (WFLEX). Plots are aligned on grasp onset (time = 0 ms). Each *gray line* is a single trial. *Bold line* is the average across trials. *Dashed vertical line* represents mean reach onset, and *bar* above is $\pm$ one standard deviation

Fig. 3.

Plots of JAVs in time for all trials in one session for Monkey S (objects 3–13, 15, 18–22). **a** MCP JAVs for thumb and digits 2–5 (THMCP and MCP2–5). **b** IP JAVs for digits 2–5 (IP2–5). **c** Abduction/adduction JAVs between fingers (ABD1–4) and wrist flexion/extension JAV (WFLEX). Conventions as in Fig. 2

Fig. 4. JA and JAV ranges during premove, reach, and grasp. Range in JAs (**a, b**) and JAVs (**c, d**) during *remove*, *reach* divided into three segments (Reach 1 = 100 ms, Reach 2 = 200 ms, and Reach 3 = 300 ms), and *grasp* averaged across all sessions for Monkey S (**a–c**) and Monkey B (**b–d**)

Fig. 5. Correlations among JAs and JAVs. Average correlation coefficients between the temporal progression (all epochs) for all possible pairs of JAs (a), JAVs (b), and JAs (c) compared with JAVs for all sessions

Fig. 6. SVD results for JAs and JAVs. **a, c** Bar graphs of eigenvector coefficients for the model session (Monkey S) for SVD performed using JAs (**a**) and JAVs (**c**). Numbers in upper left are variance explained. **b, d** Mean (+standard deviation) across sessions of each eigenvectors' coefficients (absolute value) for SVD performed using JAs (**b**) and JAVs (**d**) for each monkey. Average dot product is shown in *upper left corner* of **b, d** (monkey S *top*, monkey B *bottom*)

Fig. 7.

Variance explained by EVs and hand reconstructions. **a, b** Eigenvalues for SVDs for all sessions for both monkeys. Bar graph of mean ($\pm$ standard deviation) eigenvalues (y-axis) for each eigenvector (x-axis) resulting from SVD analysis of JAs (**a**) and JAVs (**b**). *Dashed line* indicates level of variability explained by random data (7.14 %). **c, d** Mean and standard deviation of the RE for all sessions (y-axis) for SVD using JAs (**c**) and JAVs (**d**). The *black circles* are based on the standardized SVD analysis in which the average JA or JAV was removed (Stand). The *white circles* are based on the analysis in which the average JAs or JAVs was included in the RE (Non-Stand). Note the change in Y-scale for the JA reconstruction based on the two methodologies. X-axis is the number of eigenvectors used in the reconstruction. *Dashed lines* in **c** and **d** indicate levels of acceptable error (0.1)